JPS

The Journal
of the
Polynesian Society

VOLUME 131 No.3 SEPTEMBER 2022

THE POLYNESIAN SOCIETY
THE UNIVERSITY OF AUCKLAND
NEW ZEALAND

THE ORIGINS AND DISPERSAL THROUGHOUT THE PACIFIC ISLANDS OF FEHI BANANAS (*MUSA* SERIES *AUSTRALIMUSA*)

LEX A.J. THOMSON
Australian Centre for Pacific Islands Research
JEAN-FRANÇOIS BUTAUD
Independent Botanist, Tahiti
JEFF DANIELLS
Queensland Department of Agriculture and Fisheries
PAUL A. GERAGHTY
University of the South Pacific
ADRIANA HIARIEJ
Universitas Pattimura
VALÉRIE KAGY
Institut Agronomique néo-Calédonien
JEAN KENNEDY
Australian National University
ANGELA K. KEPLER
Naturalist, Hawai'i
DAVID J. MABBERLEY
Wadham College, University of Oxford; Macquarie University;
Australian Institute for Botanical Science
GABRIEL L. SACHTER-SMITH
Banana Researcher and Grower, Hawai'i
JULIE SARDOS
Alliance Bioversity-CIAT
WILLIAM H. WILSON
University of Hawai'i at Hilo
MAURICE WONG
Direction de l'Agriculture, French Polynesia

ABSTRACT: Fehi bananas are a Pacific Islands and eastern Indonesian assemblage of parthenocarpic diploid and triploid cultivars in *Musa* series *Australimusa*. Fehi cultivars were derived principally from *M. maclayi*, *M. lolodensis* and *M. bukensis s.l.* and related entities. Eleven Fehi cultivar groups comprising morphologically similar cultivars are described, along with naturalised forms from eastern Polynesia. Fehi cultivars have been referred to particular species such as *M. troglodytarum* and

---

Thomson, Lex A.J., Jean-François Butaud, Jeff Daniells, Paul A. Geraghty, Adriana Hiariej, Valérie Kagy, Jean Kennedy, Angela K. Kepler, David J. Mabberley, Gabriel L. Sachter-Smith, Julie Sardos, William H. Wilson and Maurice Wong, 2022. The origins and dispersal throughout the Pacific Islands of Fehi bananas (*Musa* series *Australimusa*). *Journal of the Polynesian Society* 131 (3): 289–335. | https://doi.org/10.15286/jps.131.3.289-335

M. fehi, but further genetic research is needed to ascertain how human-selected cultivars are interrelated and derived from any particular species.

Keywords: Australimusa biogeography, *Callimusa*, crop wild relatives, Fehi bananas, Micronesia, Polynesia, Makira Island (Solomon Islands), Tahiti, historical linguistics of Fehi, Fehi origins and dispersals

DEDICATION

This paper is dedicated to the Pacific Islanders who selected and maintained Fehi cultivars and the intrepid voyagers who sailed throughout the Pacific carrying and dispersing Fehi and many other crops; to Dr Richard Markham (1956–) for his inspirational leadership of the International Network for the Improvement of Banana and Plantain (INIBAP) (2003–2008) and as Pacific Crops research programme manager at the Australian Centre for International Agricultural Research (ACIAR) (2010–2019); and to the late Dr Lois Englberger (1949–2011) for her passionate human nutritional work in the northern Pacific, promoting the conservation and use of Karat and other Fehi bananas.

The worldwide familiarity with bananas conceals an ancient and complex history in the Asia-Pacific region, home to a rich profusion of types never seen by most consumers. The biogeographical, taxonomic and cultural histories of bananas are the subject of a huge literature that is increasingly specialised, drawing on rapidly advancing biomolecular methods as well as new insights from other fields such as archaeobotany and linguistics. This interdisciplinary research, crucial to the conservation and improvement of the world banana crop, has a long history. Its emerging consensus is rewriting earlier, oversimplified outlines of the botanical and cultural origins of cultivated bananas, revealing ever greater complexity (e.g., Cenci *et al.* 2021; Christelová *et al.* 2017; Fu *et al.* 2022; Perrier, De Langhe, *et al.* 2011; Perrier, Jenny, *et al.* 2019; Sardos, Breton, *et al.* 2021).

This paper focuses on one iconic Pacific type of banana, the Fehi banana. While bananas all belong to the genus *Musa*, Fehi bananas are botanically distinct. They were domesticated from wild ancestors belonging to series *Australimusa* (Cheesman) Simmonds (sect. *Callimusa*), while most cultivated bananas, including the commercial Cavendish, were domesticated from sect. *Musa* species[1] (all notes are provided as on-line supplementary information at https://thepolynesiansociety.org/thomson_etal_SI.pdf). Species and cultivars within series *Australimusa* are genomically different from sect. *Musa* species (Janssens *et al.* 2016; Simmonds and Weatherup 1990) and are represented by *M. textilis* Née (T genome). Both *M. textilis*—the fibre crop *abacá* ‘Manila hemp’—and Fehi bananas have received far less attention than the commercially important bananas of sect. *Musa* grown for fruit.

In the literature cited above, Fehi are hardly mentioned, yet their biological and cultural histories, including pathways to domestication and subsequent spread by people in the Pacific, are entangled with the other Pacific bananas. We include new data from recent collections and reassess the origins and spread of Fehi cultivars throughout the region. We hope that our attention to this neglected group will stimulate further research, especially much-needed comprehensive genetic, cytological and morphological assessments.

Bananas, including Fehi types, are believed to have been carried by Lapita colonists from the western Pacific into Remote Oceania, during the initial colonisation of Polynesia around 3000–2800 BP (Barrau 1959: 49; Kirch 1997: 205, 218; Kirch and Green 2001: 122–25). Kennedy (2008) pointed out that the generalised inclusion of bananas as part of the foundation of Polynesian agriculture oversimplifies the botanical complexity of multiple, distinctive lineages of Pacific banana cultivars, including, but not limited to, Fehi bananas, a complexity that is poorly reflected in a literature full of terminological confusions. She reviewed new evidence of the multiple biogeographical origins of Pacific bananas, which strongly suggests similarly complex dispersal pathways. The linguistic evidence summarised by Kirch and Green (2001: 123) distinguishes Oceanic cultivated bananas as Fehi and the rest (i.e., series *Australimusa* and sect. *Musa*, respectively). This distinction has frequently given rise to the mistaken assumptions that only Fehi bananas derive from wild species indigenous to the New Guinea region, that the sect. *Musa* cultivars were introduced from the west and that reconstructed terminologies will reflect this. But, since this simplification of the New Guinea–region bananas is no longer tenable, more detailed evidence is needed to facilitate reconstruction of the terminologies of early Lapita times. Despite much speculation, it is not known precisely which cultivars were locally available, nor which might have been imported by Austronesian-speaking colonists (Kennedy 2009a; Ross 2008).[2] The definition, chronology and distribution of Lapita sites continue to be refined and debated (Bedford *et al.* 2019). Other Pacific staple crops, notably breadfruit (*Artocarpus* spp.), sweet potato (*Ipomoea batatas* (L.) Lam.), taro (Araceae spp.) and yams (*Dioscorea* spp.), have presented similar problems of rationalising terminological and biogeographical data, as documented in a considerable body of literature (Ballard *et al.* 2005; Kennedy and Clarke 2004: 27–29; Langdon 1989; Lebot 1999; Matthews 2014; Ross 2008; Yen 1974b, 1993; Zerega *et al.* 2006).

The Fehi bananas, sometimes referred to as *M. troglodytarum* L. or *M. fehi* Bertero ex Vieill.,[3] represent a distinctive Pacific Islands, New Guinean and eastern Indonesian assemblage of cultivars in *Musa* L. series *Australimusa* (Daniells and Janssens 2021; Kagy *et al.* 2016: 8; Kennedy

2008, 2009a; Sharrock 2001; Simmonds 1959: 65–75). Häkkinen (2013) formalised reduction of genus *Musa* taxa into two sections, viz. sect. *Musa* (including Baker's subgenera *Eumusa* and *Rhodochlamys*) and sect. *Callimusa* Cheesman (including sect. *Australimusa* Cheesman and sect. *Ingentimusa* Argent (Baker 1893; Cheesman 1947, Argent 1976). Recent phylogenetic analyses strongly support two clades (Burgos-Hernández *et al*. 2019; Fu *et al*. 2022; Janssens *et al*. 2016). We have used the term series to distinguish *Australimusa* cultivars and their assumed progenitors, following Simmonds's (1959: 52; 1962: 101) usage. This monophyletic easterly distributed clade is characterised by a unique set of morphological characters (Daniells and Janssens 2021).

Series *Australimusa* bananas are characterised by more or less erect bunches of seedless edible fruits; starchy yellow-orange, sometimes greenish-tinged, pulp rich in carotene precursors; and typically a red-purple sap exudate from the cut pseudostem (MacDaniels 1947; Simmonds 1959: 65). Members of the group have a complex and unsatisfactory taxonomic history including the naming of dubious, incompletely described and/or conspecific "species",[4] and misapplication of their names (Cheesman 1949; Häkkinen *et al*. 2012; MacDaniels 1947: 15–23; Sagot 1893: 222; Simmonds 1959: 66). From the start of European taxonomic work, there has been confusion, because the bananas described by Linnaeus as *M. troglodytarum* included two entities now referred to different sections of the genus. *Musa troglodytarum* has since been lectotypified so as to be based on Rumphius's *M. uranoscopus* of 1747 and also referred to sect. *Callimusa* (Merrill 1917: 150).

Musa troglodytarum is a cultivated banana from Ambon, Buru, Haruku, Kei Besar, Saparua and Seram in Maluku Province, eastern Indonesia (MacDaniels 1947: 16), where it is known locally as *tongkat langit pendek*, *tongkat langit kecil* and *telo mata lala* (Hermanto *et al*. 2014: 5, 12). Rumphius (1747: 137) described it as having flattened, brown seeds in five or six longitudinal rows. These seeds are vestigial and non-viable according to our observations and a report in MacDaniels (1947: 16), both in accord with its triploid status (Hermanto *et al*. 2014: 5; flow cytometry analysis at the International Banana Genotyping Centre in the Czech Republic). *Musa troglodytarum* is morphologically distinct from the New Caledonian *M. fehi* Bertero ex Vieill.,[5] with which it has often been merged (MacDaniels 1947: 16–18). A stark difference is in the male inflorescence: the male peduncle of *M. troglodytarum*—based on Rumphius's *M. uranoscopus*—is pendent (Rumphius 1747: t. 61) and the male bud (or bell) is green, smooth and narrow, and up to 30 cm long (Rumphius 1747: 137), while the male peduncle of *M. fehi* is erect (Vieillard 1862: 45) and short with few (6–12) acuminate, spreading, cream to pale whitish-green bracts (and closely resembling *M. troglodytarum* var. *acutaebracteata* of MacDaniels 1947: 21). *Musa troglodytarum* has several morphological resemblances to the wild *M. lolodensis* Cheesman, from eastern Indonesia and New Guinea, making the latter a candidate ancestor of the cultigen.

Fehi bananas include both diploid and triploid cultivars[6] (Sardos, Christelová, *et al.* 2018) with 2n = 20 and 3n = 30, but few cultivars have been examined for their ploidy level. Accordingly, there is a need for the ploidy levels of more Fehi cultivars to be assessed, through flow cytometry and direct chromosome counts. By comparison with the more widespread, commercially important cultivars of sect. *Musa*, the Fehi cultivars and their relationships to wild relatives have been given relatively little attention in molecular studies (Christelová *et al.* 2017; Čížková *et al.* 2015; Davey *et al.* 2013; Fu *et al.* 2022; Jarret *et al.* 1992; Kennedy 2008; Sharrock 2001). The nearest relatives of Fehi cultivars appear to be a group of Papuasian and Australasian *Musa* species: *M. bukensis* Argent (Fig. 1)—possibly including undescribed entities such as *awawe* (Makira), *ba'u lalao* and *ba'u kokofio* (Malaita) (Fig. 2), *M. fehi*, *M. jackeyi* W.Hill, *M. johnsii* Argent*, M. lolodensis*, *M. maclayi* F.Muell. ex Mikl.-Maclay[7] (Fig. 3) and *M. peekelii* Lauterb: indeed, several of these species have previously been suggested as likely contributors to Fehi/*M. troglodytarum* (Jarret *et al.* 1992; Ploetz *et al.* 2007: 3; Sharrock 2001; Simmonds 1956: 485). Simmonds (1962) considered some of these species, and their subspecies, as rapidly evolving because of the lack of effective genetic isolating mechanisms, but often manifesting as morphologically distinguishable geographical variants. Argent (1976: 96) reported that variation in *M. maclayi* was much greater in the eastern part of its range and suggested that some populations on Bougainville had introgressed with another unknown species. This "unknown" species may be *M. bukensis*, or other possibly undescribed species in series *Australimusa* recorded from the central and eastern Solomon Islands by Daniells (2007) and Sachter-Smith (2011). Fu *et al.* (2022) suggest that the series *Australimusa* species constitute a very recent radiation associated with New Guinea orogeny. Notably, while their sample of these species is more comprehensive than earlier studies, they nevertheless comment that incomplete taxonomic and gene sampling of genus *Musa* remains a barrier to full understanding.

Fehi bananas were first domesticated in Papuasia (Kagy *et al.* 2016; Kennedy 2008, 2009b; Simmonds 1956; Smith 1979: 186) with secondary centres of domestication and selection in Micronesia and Tahiti. It is here considered that most reports of wild, fertile "*M. troglodytarum*" in the southwestern Pacific (Papua New Guinea and Solomon Islands) refer to *M. maclayi,* which produces irregular compressed seeds 6–9 mm across (De Langhe 2009: 273; Mueller 1885: 355). This includes the wild fertile forms of Fehi from Boana, near Morobe (Papua New Guinea) reported by MacDaniels (1947: 40 & t. 10B—image provided by Mary Strong Clemens (1873–1968)), which match typical *M. maclayi*. Fertile variants of Fehi from near Farino and Canala in the interior of Grande Terre, New Caledonia, appear to be referable to *M. fehi* Bertero ex Vieill. *sensu stricto*.[8]

Figure 1. *Musa bukensis* (*Australimusa*), Autonomous Region of Bougainville (Photo: Gabriel Sachter-Smith). Inset: Cut pseudostem showing purple sap exudate.

Figure 2. *Musa* aff. *bukensis* (*Australimusa*). 2a: *Awawe*, Makira, Solomon Islands (Photo: Jeff Daniells). 2b: *Ba'u lalao*, East Kwaio, Malaita, Solomon Islands (Photo: Gabriel Sachter-Smith). 2c. *Ba'u kokofio*, East Kwaio, Malaita, Solomon Islands (Photo: Gabriel Sachter-Smith).

Figure 3. *Musa maclayi* subsp. *maclayi* var. *maclayi*, Morobe, Papua New Guinea. 3a: Variation in mature bunch (infructescence). 3b: Close-up of fruits. 3c: Longitudinally cut fruit showing seeds. Photos by Axel Poulsen.

IMPORTANCE OF FEHI IN POLYNESIA AND BEYOND

Fehi are cultivated on volcanic high islands and are poorly adapted to low-lying atolls. However, they are grown on the raised coralline island of Niue, and possibly also occur on the Federated States of Micronesia atolls of Mokil and Nukuoro (Caroline Polynesian Outlier), where the local name has been borrowed from Pohnpei (Ken Regh, pers. comm., 2021). In many Pacific islands, cultivars of Fehi have traditionally been important sources of human food, as well as providing dyes and fibres for weaving; like most bananas, many parts of Fehi plants are useful (Kennedy 2009b; Kepler and Rust 2011: 259–60). In Tahiti, they became an important, if not the principal, staple food, being a major source of carbohydrate (Cuzent 1857; Henry 1928: 33; MacDaniels 1947: 5–6; Simmonds 1959: 70–71). In prehistoric times, Fehi (Tahitian *fēʻī*) cultivars were mostly planted at > 500–800 m elevation with many small gulches named *peho fei* and *Vallée à fei* ‘fē‘ī valley’ on the land register [https://www.tefenua.gov.pf/]. Nowadays, most fē‘ī fruits sold in Tahitian markets come from lowland plantations, although long-lived relicts of earlier plantings and naturalised fē‘ī survive in difficult-to-access uplands and provide fē‘ī hunters with fruit. Many fē‘ī bunches are left to go to waste and/or are consumed by feral pigs.

In other parts of Polynesia, Fehi were less important as human food, with a much smaller number of cultivars recorded and traditionally exchanged. Fehi cultivars were grown and variously used for food, fibre, dyes and medicines in the Cook Islands (Sardos, Sachter-Smith, Ghanem, *et al*. 2019; Wilder 1931: 33), Hawai‘i (Kepler and Rust 2011: 252–54; MacDaniels 1947: 44–45), the Marquesas (Jouan 1865: 45), Niue (Yuncker 1943: 37–39), Sāmoa (Whistler 1984: 481; 2000: 198) and Wallis & Futuna (Kirch 1978: 166) and on several Polynesian outliers including Rennell and Bellona (Elbert 1975). Fehi were of considerable cultural significance in Rotuma (McClatchey *et al*. 2000: 354; Harieta Bennett, pers. comm., 17 February 2021).

Fehi cultivars appear to have been rather sparingly used for human food in most parts of Melanesia, including Papua New Guinea (Kennedy and Clarke 2004: 24, tables 9 & 10; Sardos, Paofa, *et al*. 2019), Bougainville (Sardos, Breton, *et al*. 2018), Vanuatu (Walter and Sam 2002: 42), New Caledonia (Kagy 1998; Vieillard 1862: 45) and Fiji (Dodds 1946 as *M. fehi*; Seemann 1865: 29 as *M. uranoscopus*; Smith 1979: 186). An exception is Makira (San Cristobal), Solomon Islands—a notable repository of Fehi diversity—with at least nine cultivars still being grown (Daniells 2007; Daniells, Englberger and Lorens 2011; Daniells, Sachter-Smith and Taylor 2016; Englberger, Lyons, *et al.* 2010; Sachter-Smith 2011). Fehi are relatively common and remain important local food sources in Makira, but, even though they are found throughout the main Solomon Islands, they are less favoured as food than are bananas in sect. *Musa* (Yen 1974a: 257).

Apart from Fehi, another distinctive set of Pacific bananas (sect. *Musa* genome AAB),[9] including Maoli and Pōpō‘ulu sub-groups, likely originated in the New Guinea region (Carreel *et al.* 2002; Daniells 1990, 1995; Lebot *et al.* 1993; Lebot 1999). They were ancient introductions to New Caledonia, where they have great cultural significance in Kanak society (Kagy and Carreel 2004; Kagy *et al.* 2016). Fehi bananas also feature prominently in New Caledonian myths and legends, and have special cultural significance in the northeast and east (around Canala) of Grande Terre, as well as on Maré, Loyalty Islands: it was believed that as Fehi were originally found in the forest they could be the origin of all bananas in New Caledonia (Kagy 1998). Fehi have deep symbolic value as the red/purple sap is believed to be the blood of the ancestors, including in Fiji (see p. 296), and accordingly they are sometimes planted around houses for protection. The symbolism, practices and taboos depend on the clan, and associated Fehi creation myths. Red or black colours are always associated with ancestors, but sometimes with evil spirits, as in Paimboas/Ouégoa in the northeast of New Caledonia. Fehi are often subject to cultural taboos, including prohibitions on the planting and movement of suckers and on the eating of fruits, with consumption on Maré permitted only during famines (Kagy 1998).

In the Federated States of Micronesia (Chuuk, Kosrae, Pohnpei and Yap) Fehi bananas were vital traditional sources of nutrition, for example as an important infant food, while in Pohnpei they were used for traditional offerings to high chiefs (Daniells, Englberger and Lorens 2004; Englberger, Daniells, *et al.* 2018; Englberger, Darnton-Hill, *et al.* 2003). Ironically their consumption declined in some places on Pohnpei, where ill health was spuriously linked to Fehi's effect of turning urine orange-red—the latter being an indication that excess provitamin A compounds were being excreted—in communities where there was chronic vitamin A deficiency. This was addressed in the early 2000s by the Pohnpei Island Food Community, Dr Lois Englberger and Federated States of Micronesia governments, culminating in Karat being declared the State Banana of Pohnpei on 19 October 2005.

In eastern Indonesia, at least four Fehi cultivars—known locally as *pisang tongkat langit*—are used for food (Rumphius 1747: 137, 139, t. 61; Rant 1934), and have been moved and cultivated as far west as Mount Galunggung in West Java (Dwivany *et al.* 2020).

CLASSIFICATION OF FEHI BANANAS

Fehi bananas are a diverse assemblage of cultivars, morphologically and biochemically linked by their erect fruit bunches,[10] red-purple sap exudates and fruits with bright yellow-orange pulp, rich in provitamin A. In order to account for these traits we consider that the majority of Fehi cultivars have a member of the *M. maclayi* complex as the source of at least one of the parental species, as was posited by Simmonds (1956: 485) and De Langhe *et al.* (2009: 169). In other words, Fehi cultivars are considered as mainly comprising a set of selected parthenocarpic clones of *M. maclayi s.l.*[11] and their hybrids with other *Musa* species.

Kepler (2011) determined that major morphological variations among Fehi bananas enable provisional division into nine subgroups. Since 2011, additional banana-collecting expeditions in the South Pacific Islands (e.g., Sardos, Breton, *et al.* 2018; Sardos, Sachter-Smith, Ghanem, *et al.* 2019; Sardos, Sachter-Smith, Shandil, *et al.* 2019; Sardos, Paofa, *et al.* 2019), unpublished genetic and cytological studies and our research for this paper have enabled these subgroups to be revised,[12] as elaborated in the following descriptions. Using the International Code of Nomenclature for Cultivated Plants, we employ the term cultivar group, rather than subgroup, to aggregate morphologically similar and putatively related cultivars in 11 cultivar groups, a naturalised or wild, seeded group being the 12th, as described below and illustrated in Figs 4–15.

Diploid Cultivar Groups[13]

1. ‘Aiori [14]

Ploidy: Diploid.

Pseudostem: 4.5–5.5 m tall,[15] slightly swollen near base, slender (25–35 cm ⌀ near base) then slightly tapering, green without with magenta underlayers, weathering grey-tan or light pinkish-brown, peeling near base, glazed black at base (to 0.6–0.1 m).

Figure 4. Fehi cultivar group ‘Aiori. 4a: *Toraka fagufagu*, Makira, Solomon Islands (Photo: Jeff Daniells). 4b: *‘Aiori*, Hawai‘i, USA (Photo: Forest and Kim Starr). 4c: *‘Aiori piripiri*, Tahiti, French Polynesia (Photo: Maurice Wong). 4d: *‘Aiori varavara*, Nuku Hiva, Marquesas, French Polynesia (Photo: Jean-François Butaud). 4e: *Limot*, Buka Island, AR Bougainville (Photo: Gabriel Sachter-Smith). 4f. *Säe*, Rotuma (Photo: John Bennett).

Inflorescence: Male peduncle erect, short approx. 30 cm long; inflorescence bracts lanceolate, deciduous; typically < 10–25 bract scars, ± terminal, bulbous organ (greenish-yellow with greyish cap).

Infructescence: Bunch elongated/rounded trapezoidal, with 6–12 hands. Fruits (20–) 40–60 (–90) per bunch ± compact/tight, but more open in *'aiori mā'a āteatea*, *'aiori mā'a varavara*, *toraka parao*. Fruits typically ≤ 12–15 cm long × 4–6 cm ⌀ (up to 18 cm long × 7 cm ⌀ in basal fruits), pedicellate (pedicel ± 4–5 cm long), 3- to 5-angled, ± rounded near apex; style persistent (with curly spent matchstick appearance), apical fruits with persistent beak formed from united flower parts, pericarp yellow-green turning yellow to orange-red with linear-tessellated brownish cracks at maturity, then black and coppery red; ± persistent style (deciduous or short to approx. 5 mm long, curly). Infrequently with viable seeds.

Cultivars/distribution: *Lolu*, *wore* (West New Britain Province, Papua New Guinea), *limot*, *poso-olohi* (Buka, Bougainville), *toraka parao*, *toraka fagufagu* (Makira, Solomon Islands), *soaqa* (Fiji), *säe* (Rotuma, Fiji), *ausulasula* (Sāmoa), *hulahula* (Niue), *'aiori* (ten cultivars, Tahiti, French Polynesia), *'ārutu* (Tahiti, French Polynesia).

2. Baubaunio

Ploidy: Diploid.

Pseudostem: 4–5.5 m tall, stout at base (40–45 cm ⌀), tapering to 30 cm ⌀ (*ha'a*, *djan*) to 6–8 m tall (e.g., *'ā'ata*, *rūreva, toro a'ia'i*); purplish-black at base, grey or greyish-brown in middle, and green apically.

Inflorescence: Male peduncle erect, short. Bracts sharply pointed, green without and cream to pale green within, 6–12 evident in unopened bud, not evenly distributed, deciduous; at maturity the male peduncle reduced to very short, scarred stem (10–15 bract scars), ± few floral remains—truncate, greenish-yellow bulbous stub(s) with a grey-black cap.

Infructescence: Roughly triangular, ± open arrangement of fruits in 8–10 hands; 35–40 (–60) fruits per bunch, largest fruits proximal 15–25 cm long × 3.5–4.7 (–5.5 cm) ⌀, ± strongly angular to cylindrical (at full maturity), fruits allantoid, ± narrowing towards apex with apices curving upwards. Fruits ± sessile or very shortly pedicellate (pedicel 2–4 mm). Infrequently with viable seeds.

Cultivars/distribution: *Toraka baubaunio* (Makira, Solomon Islands), *djan* (Grande Terre, New Caledonia), *'ā'ata*, *toro a'ia'i*, *ha'a, mahani*, *rūreva* (Society Islands, French Polynesia).

Figure 5. Fehi cultivar group Baubaunio. 5a: *Toraka baubaunio*, Makira, Solomon Islands (Photo: Lois Englberger). 5b: *'Utū tūroa*, Rarotonga, Cook Islands (Photo: Gabriel Sachter-Smith). 5c: *Mahani*, Tahiti, French Polynesia (Photo: Maurice Wong).

3. Bonubonu

Ploidy: Unknown (presumed diploid).

Pseudostem: 5–6 m tall, slender (15–20 cm ⌀ near base), uniformly tapering; black at base, then mid-dark green, weathering greyish-tan above.

Figure 6. Fehi cultivar group Bonubonu. 6a: *Toraka bonubonu*, Makira, Solomon Islands (Photo: Jeff Daniells). 6b: *'U'ururu*, Tahiti, French Polynesia (Photo: Maurice Wong). 6c: *'U'ururu*, Lavatubes, Tahiti, French Polynesia (Photo: Jean-François Butaud).

Inflorescence: Male peduncle erect, short (< 30 cm). Bracts sharply pointed, cream to pale green, deciduous; at maturity male peduncle reduced to very short, scarred stem (3–9 bract scars) ± few floral remains—truncate bulbous stubs (greenish-yellow with grey-black cap).

Infructescence: Bunch cylindrical to narrowly triangular, small- to medium-sized, open to compact, 25–45 to 100–130 fruits (fewer in *pūputa*); fruits ovoid, ± slightly angled, 7.5–12 cm long × 4–6 cm ⌀ (smaller near apex in *ʻuʻururu*), shortly pedicellate approx. 1 cm long, dark orange pericarp ± brownish markings; deep yellow flesh. Old pistils present on near-mature fruits as tiny protruding nipples or resembling curly spent matchsticks, but absent in mature and over-mature fruits.

Cultivars/distribution: *Toraka bonubonu* (Solomon Islands), VUT151 (Vanuatu), *pūputa* (Niue, Sāmoa), *ʻuʻururu* (Tahiti, French Polynesia).

4. Kourai

Ploidy: Diploid.

Pseudostem: 4–5 m tall, rather slender (approx. 20 cm ⌀ near base) and gently tapering; dark green, weathering pale whitish-brown or yellow-orange brown.

Inflorescence: Male peduncle erect, short (< 30 cm long); bracts lanceolate, cream but ageing brown; 12–15 bract scars.

Infructescence: Bunch broadly top-shaped. Fruits ± open arrangement of 15–25 fruits, with tendency to fall off easily at maturity; hands 3–6; proximal

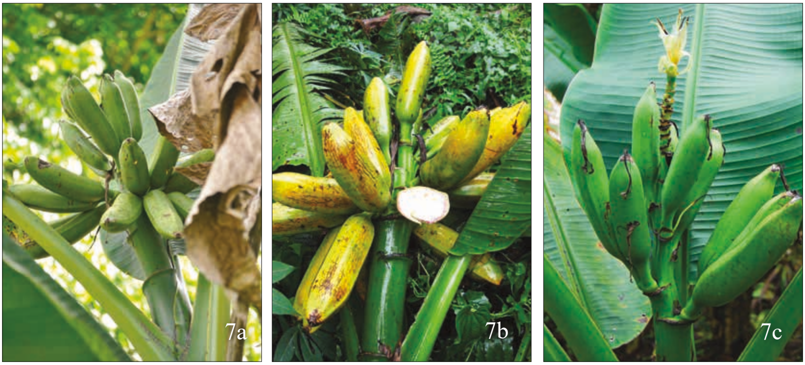

Figure 7. Fehi cultivar group Kourai. 7a: *Kourai*, Solomon Islands (Photo: Gabriel Sachter-Smith). 7b: *Torres*, Vanua Lava, Vanuatu (Photo: Fabien Cormier). 7c: *Toraka gatagata*, Solomon Islands (Photo: Gabriel Sachter-Smith).

fruits largest 15–25 (–30) cm long × 3.5–4.7 cm ⌀, ± strongly angular to cylindrical (at maturity), basal fruits ± apices curving upwards or straight, ± sessile or shortly pedicellate (pedicel 2–4 mm long).

Cultivars/distribution: ?*Kateen* (Manus Island, Papua New Guinea), ?*utafan* (New Ireland, Papua New Guinea), *kourai* (Bougainville), *toraka gatagata* (Makira, Solomon Islands), *hoaka/hereibuero*, *ota* and *ota 2*, *sawak*, *sokamé*, *Torres* (Torba Province, Vanuatu), *'oe'oe* (Tahiti, French Polynesia).

5. Menei

Ploidy: Diploid.

Pseudostem: 4.5–5 m, moderately stout, approx. 40 cm ⌀ at base, tapering strongly and uniformly to apex; green, weathering light greyish-brown.

Inflorescence: Male peduncle erect, stout, short ≤ 25 cm long, bracts deciduous, absent at maturity or with 1 or 2 floral remains on < 15–20 cm scarred stem.

Infructescence: Bunch obturbinate of 7–9 hands and 35–45 (–70) fruits, allantoid, angular, in rather open arrangement, 20–25 cm long × 6–7 cm ⌀, subsessile to shortly pedicellate, yellow turning coppery brown at maturity with yellow edges.

Cultivars/distribution: *Menei* (Manus Island, Papua New Guinea), *tongkat langit* (Ambon, Seram and Java, Indonesia).

Figure 8. Fehi cultivar group Menei. 8a: *Menei*, South Johnstone Research Station, north Queensland, Australia (cultivated, ex Manus Island, PNG) (Photo: Jeff Daniells). 8b: *Tongkat langit*, Panjang, Seram, eastern Indonesia (Photo: Adriana Hiariej).

6. Naturalised

Ploidy: Diploid.

Pseudostem: 2–4.5 m tall, ± slender, slightly swollen near base, green without, with magenta underlayers, weathering grey-tan; shiny black at base (for 0.6–0.9 m).

Inflorescence: Male peduncle erect, stout, short. Bracts sharply pointed, deciduous.

Infructescence: Bunch irregularly shaped, generally < 20 variable shaped fruits which resemble cultivars in the ‘Aiori group. Variably seeded depending on environmental factors, fruits ± filled with well-developed, viable seeds approx. 3 mm diameter.

Figure 9. Naturalised or wild fē‘ī. 9a: Fē‘ī in Upper Punahitahi Valley, South Tekou, Fatu Hiva, Marquesas, French Polynesia. 9b: Naturalised or wild fē‘ī near Viriviriterai, Tahiti, French Polynesia. Photos: Jean-François Butaud.

Cultivars/distribution: Variants ± seeded found wild or naturalised in high elevation locations in French Polynesia: Marquesas (*huetū kakano* on Nuku Hiva; *huetū popoi*, *fio*, *‘oma‘o*, *nafa* on Fatu Hiva), Tahiti (*fē‘ī ‘iri‘iri*) and Ra‘iātea (*fē‘ī ‘ōfa‘i*). Further field, propagation/seed viability, genetic and cytogenic research may indicate that these wild, seeded populations constitute environmental (high-elevation) variants of the ‘Aiori group.

7. Tāti‘a

Ploidy: Diploid.

Pseudostem: 5–7 m, 50–60 cm ⌀ at base, green-black at base weathering to pale grey-brown.

Inflorescence: Male peduncle ± pendulous, 1–2 m long. Bracts blunt or rounded at tip, ≥ 30, evenly imbricate in large, green, broad-lanceolate bud; mature bracts drying light brown, persistent, but may be weathered off near the base of the peduncle.

Infructescence: Bunch cylindrical, with 12–15 hands and comprising 100–150 tightly packed fruits, angular, scarcely tapering, 14–19 cm long × 4–6 cm ⌀, apical ones less angular and not tapered; pericarp bright coppery orange, cracks few or absent.

Cultivars/distribution: Unnamed/“Mt. Popomanaseu” (Solomon Islands), *tāti‘a*, *‘āfara tārere* (Tahiti, French Polynesia), *vē‘ī o‘oka*, *‘ūatū pīvai* (Cook Islands). (?Parthenocarpic selections of *ba‘u lalao* or *ba‘u kokofio* from East Kwalo, Makira, Solomon Islands.[16])

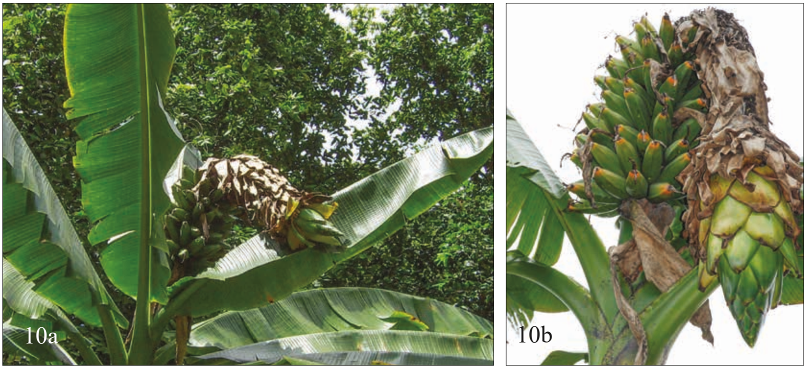

Figure 10. Fehi cultivar group Tāti‘a. 10a: *Tāti‘a*, Tahiti, French Polynesia (Photo: Quito Braun-Ortego). 10b: *‘Āfara tārere*, Tahiti, French Polynesia (Photo: Maurice Wong).

Triploid Cultivar Groups

8. Rimina

Ploidy: Triploid.

Pseudostem: 6–7 m tall, medium-slender; younger stems dark maroon near base and dark green above, older stems green, ageing to greyish-brownish near base.

Inflorescence: Male inflorescence erect, 30–50 cm long. Bud lanceolate with slightly overlapping bracts and approx. 8 acuminate bracts; proximal bracts obtuse, lanceolate, recurving before falling; bract scars, 25–30, not very prominent.

Infructescence: Bunch cylindrical or with slight apical tapering, flattened top, with 10–11 compact hands and 65–100 fruits 14–15 cm long × 4.5–5 cm ⌀, angled; pericarp yellow, turning orange-coppery ± cracks in skin. Flesh yellow orange.

Cultivars/distribution: *Rimina* (Eastern Highlands Province, Papua New Guinea), *‘āfara potopoto* and *paru* (Tahiti, French Polynesia).

Figure 11. Fehi cultivar group Rimina. 11a: *Rimina*, South Johnstone Research Station, north Queensland, Australia (cultivated, ex Eastern Highlands, PNG) (Photo: Jeff Daniells). 11b: *‘Āfara potopoto*, Kaua‘i, Hawai‘i, USA (Photo: Angela Kepler).

9. Asupina

Ploidy: Triploid.

Pseudostem: 3.5–4.5 m tall. Slender (20–25 cm ⌀ near base), very slightly tapering, mainly green with some irregular blackish patches and streaks, ageing light brown.

Inflorescence: Peduncle ≥ 0.30–0.55 m long, pendulous. Bud turbinate, dull. Bracts enclosing broad lanceolate, cream to pale brown, overlapping at apex, revolute before falling; bract deciduous at maturity, scars conspicuous, without floral remains.

Infructescence: Bunch globular-ovoid to irregularly shaped; 5–20 kg with 5–11 open hands and ± 30–45 fruits, 14–20 cm long × 5–6 cm ⌀, pedicellate (pedicel 1.5 cm long), slightly ridged/allantoid, apex rounded or slightly tapered; pericarp yellow-green turning bright orange with coppery cracks when fully mature; flesh dark yellow to orange, with very high levels of carotenoids.

Cultivars/distribution: *Asupina* (West Sepik Province, Papua New Guinea) syn. *skai* (near Kiunga, Western Province, Papua New Guinea), *tongkat langit Papua* (Manokwari, West Papua Province, Indonesia).

Figure 12. Fehi cultivar group Asupina. 12a: *Asupina*, South Johnstone Research Station, north Queensland, Australia (cultivated, ex West Sepik, PNG) (Photo: Jeff Daniells). 12b: *Tongkat langit Papua*, Manokwari, West Papua, eastern Indonesia (Photo: Agus Sutanto).

10. Karat

Ploidy: Triploid.

Pseudostem: (4.5–) 6–7 m tall, approx. 30 cm ⌀ near base, approx. 15 cm ⌀ (at 1.5 m), slender/gently and uniformly tapering; green, weathering grey-tan on lower trunk.

Figure 13. Fehi cultivar group Karat. 13a: *Usr kulasr* (syn. *karat*), Kosrae, Federated States of Micronesia (Photo: Lois Englberger). 13b: *Pouti'a*, Waimea Gardens, Hawai'i, USA (Photo: Angela Kepler). 13c: *Karat*, Pohnpei, Federated States of Micronesia (Photo: Jeff Daniells). 13d. *Pouti'a*, Hawai'i, USA (Photo: Christopher Carter).

Inflorescence: Male peduncle, erect, approx. 0.5 m long; bud large, green-yellow; bracts imbricate, broad-lanceolate/ovate, turning light yellowish-cream and brown before being shed.

Infructescence: Bunch broadly oval to round, rather open, with 3–15 (–30), or rarely even approx. 40 large ± ovoid fruits in few hands, shortly pedicellate (pedicels ≤ 5 mm), rounded at maturity, typically 18–22 cm long × 10–14 cm ⌀; L:W < 2–2.5) or slightly angled.

Cultivars/distribution: Predominantly found in Micronesia; *karat pako*, *karat pwehu*, *karat kole* (Federated States of Micronesia), unnamed/Bauro Central (Makira, Solomon Islands), ?*navis nouel* (Malekula,Vanuatu), *pouti ʻa* (Tahiti, French Polynesia—where likely extirpated).

11. Sar

Ploidy: Triploid.

Pseudostem: Massive, 6–7.5 m tall, 40–50 cm ⌀ near base, approx. 30 cm ⌀ at 1.5 m, strongly and uniformly tapering to apex; green, weathering brownish near base.

Inflorescence: Female and male flowers subtended by very large, broad-lanceolate (approx. 0.5 m long) green or purplish-green bracts; bracts drying

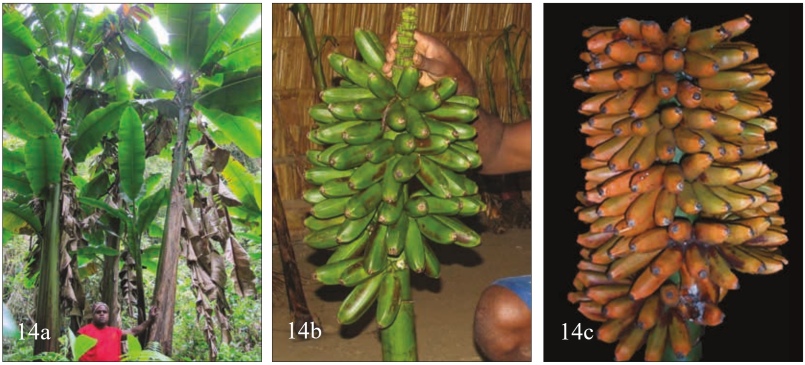

Figure 14. Fehi cultivar group Sar. 14a: *Namaco ni du*, Maré, New Caledonia (Photo: Julien Drouin). 14b: *Toraka warowaro*, Makira, Solomon Islands (Photo: Jeff Daniells). 15c: *Utimwas*, Pohnpei, Federated States of Micronesia (Photo: Lois Englberger).

brownish ± persistent but mostly shed when bunch is mature. Male peduncle erect, stout, usually ≤ 20 cm long and absent at maturity.

Infructescence: Bunch cylindrical or with slight apical tapering, flattened top or with few erect fruits, 15–30 kg, with 18 or 19 compact hands with approx. 130 fruits 10–15 cm long × 4–6 cm ⌀, ovoid, slightly angled (rounded to angular); pericarp yellow, turning orange-coppery, sometimes with maroon tints and cracks at full maturity; flesh yellow orange to deep orange.

Cultivars/distribution: *Sar* (Manus Island, Papua New Guinea), *utin iap* and *utimwas* (Pohnpei, Federated States of Micronesia), *arai ni ngir* (Yap, Federated States of Micronesia), *toraka warowaro* (Makira, Solomon Islands), *namaco ni du* (Maré, New Caledonia). (Note: its morphological appearance suggests it may be a parthenocarpic/autotriploid selection of *M. maclayi* subsp. *ailuluai.*)

12. Tongkat Langit Pendek

Ploidy: Triploid.
Pseudostem: 3–4 m, slender, green weathering brown.

Inflorescence: Erect female section, then semi-pendulous to pendulous, ≥ 1 m long with numerous conspicuous bract scars bud lanceolate to ovoid,

Figure 12. Fehi cultivar group Tongkat Langit Pendek. 15a: *Tongkat langit pendek*, Seram, eastern Indonesia (Photo: Adriana Hiariej). 15b: *Telo mata lala*, Seram, eastern Indonesia (Photo: Jeff Daniells).

≥ 12–15 cm long, shiny, green; bracts ≥ 30 enclosing male inflorescence blunt or apically acuminate, imbricate in bud.

Infructescence: Bunch ± cylindrical or irregular, small to medium, up to approx. 15 kg, with 5–13 loosely to tightly packed hands and 25–120 fruits, 10–12 cm long × 4–6 cm ⌀, slightly angled, blunt to pointed apex; pedicellate (pedicel approx. 1 cm long); pericarp yellow-orange, with brown cracks and marks at full maturity; flesh yellow.

Cultivars/distribution: Comprises two distinct variants (*tongkat langit pendek*, *telo mata lala*) from eastern Indonesia, one of which is referrable to *M. troglodytarum* L. *sensu stricto.* A cultivar similar to *telo mata lala* but with male buds degenerating before maturity has been noted in Manokwari, West Papua Province, Indonesia (Edison *et al.* 2002). (Note: its distribution and appearance suggest this cultivar group may have arisen as a parthenocarpic/autotriploid selection of *M. lolodensis* and/or parthenocarpic selection of *M. maclayi* × *M. lolodensis.*)

Representative fruit bunches and individual hands/fruits of each Fehi group are shown in Figs 4–15, illustrating the morphological variation displayed among Fehi groups, and the different cultivars in each group as indicated by country/island group in Table 1. (provided as on-line supplementary information at https://thepolynesiansociety.org/thomson_etal_SI.pdf)

ORIGINS OF FEHI CULTIVARS AND CLUSTERING OF CULTIVAR DIVERSITY

Domesticated bananas have edible fruits with few or no seeds or with non-viable vestigial seeds. They are parthenocarpic, developing pulp-filled fruits without pollination. Such fruits sometimes have occasional seeds, while the plants bearing them sometimes produce viable pollen. The male and female sterility of many cultivars has been caused by complex mechanisms acting in addition to parthenocarpy; both genetic and environmental factors are likely involved (Kennedy 2008: 77; Simmonds 1962). In sect. *Musa*, parthenocarpy is believed to be driven by a major dominant gene interacting with minor genes (Simmonds 1953). Female sterility is a variable secondary trait closely linked to banana domestication: total seedlessness can be due to the lack of surrounding pollen for effective pollination rather than to the absence of female fertility (Sardos, Rouard, *et al.* 2016). Human selection and vegetative propagation have ensured the survival and spread of domesticated bananas, including Fehi. These human interventions seem to have occurred in parallel but independently in series *Australimusa* and sect. *Musa* (Simmonds 1962: 151). Most Fehi cultivars are parthenocarpic and seedless. However, a few (naturalised forms) do produce viable seeds in New Caledonia (Vieillard 1862: 45)[17] and French Polynesia (Nadeaud 1873: 39).[18]

Due to high levels of sterility, many banana cultivars—Fehi and others—are considered to be selections derived from a single clone (Simmonds 1959). For example, the genetic diversity of 30 mostly West African plantains (*Musa* AAB genome subgroup, sect. *Musa*) constituting a representative sample of the phenotypic diversity appears to have been derived through somatic mutation and clonal diversification of a single seed/original plant (Noyer *et al.* 2005). Similarly, phenotypic diversity is high in the culturally important Maoli-Pōpō‘ulu subgroup, but genetic diversity is low (Kagy *et al.* 2016). Concurring with Simmonds (1959: 72), we suspect this also applies to Fehi cultivars, with much of the cultivar variation arising from somatic mutation and/or epigenetic variation, along with hybridisation, polyploidy and parthenocarpic cultivar selection. Where the Fehi cultivars are grown together on a large scale—such as in Tahiti, Federated States of Micronesia and Makira—and especially when some have not entirely lost seed-producing capability, there is potential for hybridisation between cultivars. However, the paucity of bird pollinators in French Polynesian forests—especially the Society Islands and Marquesas, which did not originally[19] have the tiny, efficient pollinator birds (genus *Zosterops* or white-eyes)—could have affected the degree of seediness in Fehi. This, combined with those partially seedless cultivars brought and cultivated by Polynesian settlers, would have encouraged seedlessness and increased palatability.

Our identified clusters of morphologically similar Fehi cultivars (groups) most likely originated through single connected events (hybridisation/autopolyploidy/allopolyploidy) followed by selection, cultivation and subsequent mutation and vegetative propagation of a whole suite of closely related clones. However, some proposed Fehi groups, such as the diverse ‘Aiori group, may comprise cultivar selections derived from the same or similar hybrid combinations. Further sample collection and DNA analysis is required to define these Fehi groups better and determine their genetic origins: this will surely lead to further refinement and likely reveal more cultivar groups. These could include additional groups from Makira (Solomon Islands) such as *toraka akeakesusu* or *toraka morikera* as well as from other less well-known Fehi cultivars from Bougainville, Papua New Guinea, Fiji (including Rotuma) and Maluku (Indonesia).

POSTULATED ANCIENT MOVEMENT OF *MUSA* SERIES *AUSTRALIMUSA* AND DOMESTICATION OF FEHI CULTIVARS

Two distinct groups of people are commonly distinguished in Papuasia: the earliest settlers, arriving ≥50,000 years BP from southeast Asia, usually designated Papuans, and then, much later, ≥3500 years BP, Austronesians who came from Taiwan and had moved through the Philippines and along the northern New Guinea coast to the Bismarck Archipelago.[20] Much of the accumulating genetic evidence that describes these people is necessarily based upon samples drawn from living groups, variously categorised according to geography, language and cultural history. Rare samples of ancient DNA are being added to the increasingly complex picture, notably from Lapita-associated burials in Vanuatu and Tonga, which appear to group with East Asian rather than New Guinea–area modern populations (Skoglund *et al.* 2016). However, later studies with larger samples show that in Vanuatu, the early Lapita population was very soon followed by others related to modern New Guinea/Bismarck groups (Lipson *et al.* 2018; Posth *et al.* 2018). The oversimplified residual category "Papuan" is now being deconstructed, revealing complex interrelations within New Guinea, the Bismarcks and Solomons, and all of these with neighbouring areas including Remote Oceania (Brucato *et al.* 2021; Pedro *et al.* 2020; Sheppard 2019, 2022). Most recently, samples of ancient and modern human DNA from central and western Micronesia have added further complexity, suggesting differentiation among ancient populations in the Bismarcks, with Manus (linked to coastal New Guinea) separated from New Ireland–New Britain, and all of these having multiple links with western and central Micronesia, in the post-Lapita period (Liu *et al.* 2022).

It is probable that many groups contributed to the domestication of Fehi cultivars in Papua New Guinea (PNG), especially around the Bismarck Archipelago. The postulated Fehi ancestor, *M. maclayi*, is a widespread wild species in PNG and the Solomon Islands in seral communities, including old gardens, but is nowhere purposefully cultivated (see, e.g., Argent 1976; Lentfer 2009; Simmonds 1959; Moses Pelomo, pers. comm., 5 July 2021). Through studies using diagnostic seed phytoliths, Lentfer (2009: 248) and Lentfer *et al.* (2010) have confirmed the presence of sect. *Australimusa* bananas at an early Holocene archaeological site (FIF/4, Yombon airstrip) in southwest New Britain, PNG. Lentfer *et al.* (2021: 99–100) also recorded a seeded sect. *Australimusa* banana (volcaniform leaf morphotypes and tabular seed morphotypes) from a Lapita site (dated at 3185–2639 BCE), Nenumbo, Te Motu Taibä/Ngaua, Reef Islands, Temotu Province, Solomon Islands. Lentfer *et al.* (2021: 102) found a relatively high percentage of Musaceae leaf phytoliths in the younger layer but an absence of Musaceae seed types, and suggested wild species of *Musa* were replaced by seedless domesticated bananas, including sect. *Musa* cooking bananas (plantains).

The fruits of the putative wild progenitors of Fehi cultivars are favourite foods of hornbills and are also taken by fruit bats and corvids in Papua New Guinea and the Solomon Islands. In Choiseul, Solomon Islands, *kalo* (*M. maclayi*) has viable seeds, and many germinate at the base of banana mats[21] or in rainforest canopy clearings or close to banyan (*Ficus* spp.) trees, which provide another favoured food of hornbills (Moses Pelomo, pers. comm., 15 February 2021). Solomon Islanders hunt hornbills for food, so hunters often seek out stands of wild bananas: this greatly increases their opportunity for coming across parthenocarpic forms/hybrids which have potential for human consumption, and then bringing them into cultivation through moving suckers into village gardens. Accordingly, we postulate that parthenocarpic Fehi cultivars may have been first selected from regeneration of members of the *M. maclayi s.l.* complex in rainforest openings in the eastern third of northern New Guinea, Bismarck Archipelago, Bougainville and Solomon Islands. This hypothesis chimes with the ideas of Simmonds (1956: 485), who wrote that "*M. maclayi* … is the probable major (and perhaps even only) source of the *fehi* group of edible bananas".

Species related to Fehi cultivars, such as *M. maclayi* and *M. peekelii*, have intermediate seed storage characteristics and lose viability within weeks or months of storage and drying (Kallow *et al*. 2020). Nevertheless, some *Musa* seeds (sect. *Musa*) appear able to survive for many years in the ± moist and uniform moderate (20°–25°C) temperature of a shaded rainforest soil seed bank, and this likely applies to seeds of series *Australimusa*. Where present, the seeds in most Fehi cultivars are small, irregular, shrivelled and lacking an embryo (e.g., MacDaniels 1947: 13). While seed is the most convenient form of germplasm for long-distance transport of plants on voyaging Polynesian canoes, we argue that the movement of the Fehi cultivars/clones and indeed other "canoe plants" was principally, if not exclusively, in the form of vegetative propagules. This assertion is made on the basis that:

- Fehi cultivars seldom produce viable seeds (usually only at high elevations);
- Based on storage behaviour of *M. maclayi* seeds, any seeds are likely to have a short storage life and be sensitive to desiccation (Kallow *et al.* 2020);
- Seedlings are difficult to propagate and grow slowly;
- Seedling bananas may not come true to type; and
- There is a considerable interval, at least two years, from seed/seedling to producing fruits and providing a source of human food, whereas a transplanted sucker will usually fruit within one year.

We postulate that at least two Fehi clones (from northern New Guinea/Bismarcks/Bougainville/Solomon Islands) were widely dispersed in the Pacific Islands, both north to Micronesia (Chuuk, Kosrae, Pohnpei and Yap) and south/east to Vanuatu, New Caledonia, Fiji and Sāmoa during the Lapita era beginning ca. 3500 BP (Fig. 16). These clones would have been from the two distinctive cultivar groups Karat and Sar. Both of the original cultivars appear to have been more widely cultivated and used in Micronesia than in Fiji and central-western Polynesia, with each generating three modern cultivars/clones in Micronesia, viz. *karat pako*, *karat pwehu* and *karat kole* in the Karat group and *utin iap*, *utimwas* and *arai ni ngir* in the Sar group.

A cultivar in the Menei group appears to have been moved westwards, possibly in similarly ancient times, from the Bismarcks to eastern Indonesia, where a related cultivar, *tongkat langit*, was selected and grown in Ambon and Seram, and subsequently moved even further west as far as Mount Galunggung in West Java (Dwivany *et al*. 2020).

Outside Micronesia, representatives of the Karat group appear to be rare and only survive with certainty as a few cultivated mats of the Fehi cultivar *pouti'a* in Hawai'i (recently introduced there from Tahiti). One of the Fehi cultivars (*navis nouel*) observed by Cormier (2010) in Malekula (Vanuatu) appears to be a member of the Karat group, as does a cultivar that grows at Bauro Central in the highlands of Makira, Solomon Islands (Michael Pennay; https://www.inaturalist.org/observations/4152943).

ORIGIN OF FEHI CULTIVARS IN EASTERN POLYNESIA

Tahiti was an eastern Pacific hotspot for Fehi diversity, with at least 20 named cultivars of fē'ī including at least nine of 'Aiori. This diversity is quite remarkable given the vast distance, around 5,000–7,000 km, from the posited origins of the Fehi bananas in Papua New Guinea/Solomon Islands, and especially given the apparent lack of Fehi diversity on island archipelagos, such as Fiji and Sāmoa, between them.

In reviewing the origin of the founder clones of fē'ī in Tahiti, we identified Makira (San Cristobal) and Malaita, Solomon Islands, as likely sources, given that both islands have extant cultivars in the Fehi cultivar groups that have proliferated and/or are present in Tahiti (viz. 'Aiori, Baubaunio, Bonubonu and Kourai). Furthermore, undescribed Solomon Islands species related to *M. bukensis*, viz. *awawe* (Makira), *ba'u lalao* and *ba'u kokofio* (Malaita), are morphologically similar to cultivars in the Tāti'a group and could be their direct ancestors.

Accordingly, we argue that Tahiti's founding fē'ī cultivars originated from the Solomon Islands, rather than the closer Sāmoa or Fiji. These Fehi clones (or progenitor wild species) would likely have been moved as carefully packaged sucker material,[22] directly or nearly so, via the traditional pathway from the southeast Solomon Islands Polynesian Outliers through the northern Polynesian Outliers. From the central northern Polynesian Outliers the clones could have been carried on to the Marquesas and/or Society Islands (over ca. 7–8 weeks), ca. 900–1000 years BP in accordance with the East Polynesian settlement hypothesis of Wilson (1985, 2012, 2018, 2021).

The extraordinary Tahitian fē'ī cultivar diversity originally derives from at least four or five ancestral sources: members of the morphologically similar, likely related 'Aiori, Baubaunio, Bonubonu and Kourai groups (at least 18 cultivars) and the Tāti'a (*tāti'a* and *'āfara tārere* cultivars) and Rimina (*'āfara potopoto* and *paru* cultivars) groups. It is interesting to reflect on

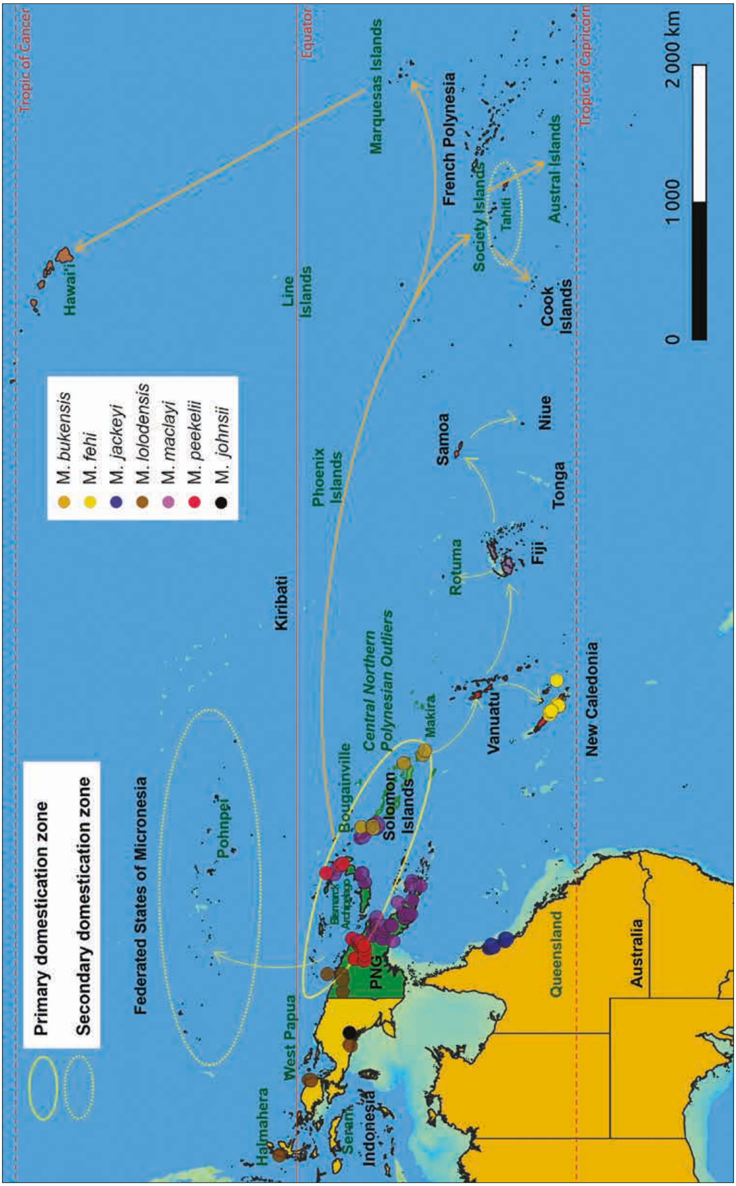

Figure 16. Map of the Pacific Islands from eastern Indonesia to Tahiti showing natural distributions of wild (*M. bukensis*, *M. jackeyi*, *M. lolodensis*, *M. maclayi*, *M. peekelii*) and naturalised species (*M. fehi*), early dispersal of Fehi from Papuasia to Micronesia and to the southeast and later dispersal from Outliers/Solomon Islands to East Polynesia, and primary (Papuasia) and secondary (Micronesia and Tahiti) centres of Fehi domestication.

why there is such fē‘ī cultivar diversity in Tahiti. It is considered that the extensive fē‘ī plantation area, from sea level to more than 1,000 m, of the original and subsequent clones provided a large base in which mutations could arise, and then be selected and propagated by observant Tahitian fē‘ī growers. The native forests in Tahiti are rather low and open, with few highly competitive tree species, and are well suited to recruitment and spread of fē‘ī. Fē‘ī hunters collecting fruit bunches from naturalised populations for food would have been well placed to identify any promising new bananas and bring them into cultivation.

There is one representative of the Karat group known from Tahiti, viz. *pouti‘a*, but this cultivar has always been rare, presumably little cultivated as it was not considered good eating (MacDaniels 1947: 32–33) or productive and is now likely extinct (Kepler and Rust 2011: 264). It is possible that *pouti‘a* is a relatively recent (e.g., past 200–300 years) Polynesian and/or post-European introduction from Sāmoa. However, the possibility of a Karat group cultivar being introduced from Makira via the pathway from the southeast Solomon Islands Outliers into the northern Outliers and on to East Polynesia cannot be ruled out.

In Tahiti, additional desirable and/or morphologically distinct mutations and hybrids of the original introduced Fehi clones were likely selected, propagated and spread further, including to Hawai‘i (Kepler and Rust 2011: 252–54) and the Cook Islands.

ORIGINS AND DERIVATIONS OF NAMES FOR FEHI BANANAS

The name for banana (sect. *Musa* cultivars) in Proto-Polynesian (PPn), the language spoken by the first inhabitants of Polynesia some 3,000 years ago, was **futi*,[23] which goes back to Proto-Malayo-Polynesian **punti* (Blust 1984–85: 49–50; Donohue and Denham 2009: 299–300; Perrier, De Langhe, *et al.* 2011: 11313–14). Reflexes of **futi* continue into the southeast Solomons Polynesian Outliers and all the northern Polynesian Outliers, e.g., Tikopian, Takū *futi*; and Rennellese, Sikaiana, Nukumanu, Kapingamarangi, Nukuoro *huti*. However, Proto-East Polynesian replaced **futi* with **maika*, a term of unknown origin, referring to cooking bananas (AAB genome, including Maoli, Pōpō‘ulu and Iholena subgroups), from which are derived Marquesan *meika* and *mei‘a*; Rapa Nui, Penrhyn *maika*; Hawaiian *mai‘a*; Tuamotuan, Rarotongan *meika* and Tahitian *mei‘a* and *mai‘a*.

Another banana term, **joRaga*, has a robust Proto-Oceanic (POc) reconstruction (Ross 2008: 278), meaning it was probably familiar to the Austronesian-speaking Lapita peoples.[24] **joRaga* has regular reflexes in Papua New Guinea (e.g., Middle Watut *cok*, Mumeng *jon*), the Solomon Islands (e.g., Arosi *toraga*, Sa‘a *hudi tolaka*, Vaghua *soga*), Polynesian

Outliers (Vaeakau-Taumako *hoaka*, Tikopia *soaka*), Vanuatu (e.g., Ngen *sokamé*, Nguna *soaga,* Northeast Ambae *hoaka*, Paamese *sōko*, Raga *hoaga*, Tamambo *soka*, Uripiv *jok*), New Caledonia (Nyelâyu, Kumak, Nemi *dāŋ*), Fiji (Bauan *soaqa*) and parts of central-western Polynesia (e.g., Sāmoa *soa'a*). However, glosses that specify Fehi are not recorded further west of the eastern Solomons. Ross, thus, cautions that "POc **joRaga* is glossed accordingly [as Fehi], but with a question mark, because this was the meaning of the PROc [Proto-Remote Oceanic, approximately the same as Proto-Eastern Oceanic (PEOc)] reflex but not necessarily of the POc term."

Another Polynesian Outlier Fehi term, Rennellese *togaka*, is phonologically marked as a borrowing of a term for Fehi from a Solomon Islands language, such as Arosi spoken on Makira, for which the term for Fehi is *toraka*, itself derived from PEOc **joRaga* by the distinctive retention of **R* as a liquid, whereas Fijian and Proto-Polynesian have lost this consonant. Arosi *toraka* is also marked by the distinctive reflex Arosi *t* for PEOc **j*, while Proto-Central Pacific (PCP) ancestral to Fijian and PPn reflects **j* in this word as **s* > Fijian *soaqa*, Samoan *soa'a.*[25]

While the reconstruction **joRaga* is solidly represented throughout the area as far east as Sāmoa, there is another form which is found in at least two languages. Rotuma, one of the few places where Fehi remain culturally important, has *säe*, which could be derived from PCP **saya* (or **caya/zaya*), and this has been borrowed into Futunan as *sae*, which means the plant and also *mets à base d'amidon et de bananes* 'food based on Polynesian arrowroot (*Tacca leontopetaloides* (L.) Kuntze) and bananas', probably the same as a kind of Rotuman *herhere* which contains *säe*,[26] and also *po'e* (Tahiti) and *poke* (Marquesas). Futuna's neighbour East 'Uvea (Wallis) has two terms for Fehi, which indicate different origins: *lotuma*, pointing to origin from Rotuma (Bataillon 1932) with its derivative *hu'a lotuma* 'purple' (lit. sap or juice of *lotuma*) (Rensch 1984), and *fehi* (Rensch 1984). Note that Bataillon's dictionary was based on research in the mid-nineteenth century, so much the earlier of the two. While *fehi* may look like a cognate of Tahitian *fē'ī*, it is most likely a relatively recent borrowing from Tongan, where *fehi* is 'a kind of plantain' (Churchward 1959), possibly itself a nineteenth-century borrowing from an eastern Polynesian source.

Within Fiji, a number of new names have developed for Fehi, which may be instructive. In parts of northeast Vitilevu, the name is *drāiturukawa* or *drākeiturukawa*, both meaning 'blood of Turukawa', this being a mythical bird that, every morning, woke up Degei, the chief deity of most of eastern Fiji, and was shot dead by a pair of mischievous twins. The name may refer to the sap or the colour of the water when the fruit is boiled. Another innovative name, found in Vanuabalavu, northern Lau, is *duduilagi* 'protruding to the sky'.

A distinct term for Fehi can be reconstructed for Proto-East Polynesian (PEPn), **fua-tu‘u*, with a clear derivation from **fua* ‘fruit’ and **tu‘u* ‘standing, erect’, the main characteristic that distinguishes the plant from **maika*. Proto-East Polynesian **fua-tu‘u* is reflected in Marquesan *huetū*, Mangarevan *‘uatu*, Rarotongan and Mangaian *‘ūtū* and Rarotongan *‘uatū*, which covers the two main divisions of the Central East Polynesian language subgrouping (Wilson 2021: 40, 43) followed here and shows expected vocalic reflexes for an old term that spread at an early period before European contact.[27]

Given that names derived from **joRaga* > PPn **soaka* are found as far east as Sāmoa but no further, the question arises as to whether there is any significance in the name changing to **fua-tu‘u*, literally ‘standing or erect fruit’ in eastern Polynesia. The answer is perhaps, but not necessarily so. In a study of PEPn plant names (Geraghty 2009), it was demonstrated that most plants have retained their PPn names. Examples from food plants include PEPn **ifi* [*Inocarpus fagifer* (Parkinson) Fosberg, Tahitian chestnut], **kape* [*Cyrtosperma merkusii* (Hassk.) Schott or ‘*Alocasia*’, ‘swamp taro’], **kuru* [*Artocarpus altilis* (Parkinson) Fosberg, ‘breadfruit’], **niu* [*Cocos nucifera* L., ‘coconut’], **parai* [*Dioscorea nummularia* L., ‘Pacific yam’], **pia* [*Tacca leontopetaloides*, ‘arrowroot’], **pirita* [*Dioscorea pentaphylla* Lam., ‘five-leaf yam’], **talo* [*Colocasia esculenta* (L.) Schott, ‘taro’], **tī* [*Cordyline fruticosa* (L.) A.Chev., ‘ti’], **‘ufi* [*Dioscorea esculenta* (Lour.) Burkill or *D. alata* L., ‘yam’]. Indeed, the name of only one major food plant was changed, from PPn **futi* [*Musa*, ‘banana, plantain’] to PEPn **maika*. The change of PPn **soaka* to PEPn **fua-tu‘u* and then **fekī*[28] may well indicate some kind of discontinuity, and fits with our hypothesis that Fehi in East Polynesia did not arrive via Sāmoa or central-western Polynesia.

Part of the history of *fē‘ī* in East Polynesia is the development of this distinct and now universally applied term for it in Tahiti, a locus of major cultivar diversity. The early Tahitian term *fekī* may have derived by vowel lengthening from PEPn **fekī* ‘type of tree fern’, reflected in Māori as *whekī* ‘tree fern species’.[29] The Tahitian term *fē‘ī* apparently spread in post-European times, or shortly before that, to the southern Cook Islands resulting in Rarotongan, Aitutakian, Ma‘uke *vē‘ī* and Mitiaro *ve‘i*. Southern Cook Islands *vē‘ī*, *ve‘i* are clearly borrowings because southern Cook Island languages borrow /*f*/ as /*v*/, but in directly inherited terms their glottal stop and their /*k*/ correspond to Tahitian /*f*/ and glottal stop, respectively. Note that in the Cook Islands, Rarotongan and Mangaian also reflect the older PEPn term **fua-tu‘u*, and with the expected direct inheritance phonology as *‘uatū* (the most common general term for Fehi cultivars). Terms in the Austral Islands, i.e., Rurutu *ve‘i*, Ra‘ivavae *he‘i* and Tupua‘i *fe‘i*, as well as Rapan *fe‘i*, are also likely very recent, if not post-European, borrowings from Tahitian. These areas have both a post-European and pre-European history of extensive Tahitian influence. The phonological form of the Ra‘ivavae term could possibly represent an older spread from Tahitian, but the glottal stop in *he‘i* rather than a /*k*/ suggests a recent borrowing.

Possibly related to the retention of direct reflexes of PEPn **fua-tu‘u* on Rarotonga and Mangaia within the southern Cook Islands is the fact that they are the larger southern Cook Islands, with Rarotonga having the highest elevations, and providing environments where Fehi could flourish best. As larger islands with larger populations, they were also less likely to be as quickly influenced in replacing earlier terms with borrowings from Tahitian.

A Hawaiian cognate of Tahitian *fē‘ī* is *hē‘ī* ‘papaya’ (*Carica papaya* L.). The neotropical papaya was introduced into Hawai‘i between 1800 and 1820 (Yee *et al*. 1970: 3), and the fruit shape of some papayas resembles that of certain Fehi cultivars (e.g., *karat* or *pouti‘a*). Hawaiian *hē‘ī* is a term for *fē‘ī* along with *mai‘a akua* ‘ghost/spirit/god banana’, *mai‘a kāne* ‘male banana, or banana of the god Kāne’, *mai‘a liko* ‘central leaf bud banana’ and *mai‘a polapola* ‘Tahitian banana’, where *polapola* is a post-European name for Borabora. The fact that Hawaiian *hē‘ī* corresponds to Tahitian *fē‘ī* supports the contention of Kepler and Rust (2011: 258) that *hē‘ī* arrived several times before James Cook’s visits to Hawai‘i. If the Tahitian term *fē‘ī* were a post-European borrowing, we would expect it to be pronounced in Hawaiian as *pē‘ī*, parallel to *peawini* ‘fairwind’, *palaoa* ‘flour’ and *Pakuhiwa*, the post-European contact Hawaiian name for Fatu Hiva, one of the Marquesas Islands. Hawaiian *hē‘ī* is the only East Polynesian term suggesting any antiquity for the Tahitian term *fē‘ī*. Even with evidence from Hawaiian, the term **fua-tu‘u* is better supported as the oldest East Polynesian term for Fehi.

Whilst the origin of the name *karat* for certain Fehi cultivars in Pohnpeian is uncertain, it is likely to be ancient. Frederick Christian, who visited Micronesia in 1896 during the Spanish period, recorded the name *karati* ‘the plantain’ in the Polynesian Outlier language Nukuoroan (Christian 1898), and this likely indicates that *karat* was borrowed from Pohnpeian sometime before Christian’s visit, as supported by linguistic evidence (Ken Regh, pers. comm., 2021).

NATURALISED SPECIES OF *MUSA* SERIES *AUSTRALIMUSA* IN FRENCH POLYNESIA?

The presence of ± seeded, likely naturalised Fehi in upland environments in the Marquesas and Society Islands (Fig. 10a, 10b), including *huetū kakano*, *popoi*, *fio*, *‘oma‘o*, *nafa* in the Marquesas (Nuku Hiva, ‘Ua Huka and Fatu Hiva), *fē‘ī ‘ōfa‘i* on Ra‘iātea (Leeward Islands) and variants of *‘aiori* in Tahiti, has long been noted (Jouan 1865: 45; Kepler and Rust 2011: 249; MacDaniels 1947: 13). The Fehi that grow in the remote interior of New Caledonia—presumably conspecific with *M. fehi* Bertero ex Vieill.— morphologically resemble seeded ʻAiori cultivars with their black pseudostems and small bunches of short dark-brown fruits and greenish pulp ± viable seed.

Kepler and Rust (2011) hypothesised that seeded Fehi may have been bird-dispersed—especially by *Ducula* pigeons and the now-extinct large *Cyanoramphus* parrots—in a stepped dispersal process from southwest Melanesia to eastern Polynesia. However, there are no records of seeded Fehi bananas growing in uncultivated settings in central Polynesia. The disjunct presence of wild, seeded New Guinean (and Queensland) *M. acuminata* subsp. *banksii* (F. Muell.) N.W.Simmonds (sect. *Musa*) in Sāmoa (Sardos, Sachter-Smith, Shandil, *et al.* 2019), a distance of approx. 5,000 km, provides some support for long-distance dispersal of seeded bananas in the South Pacific: the local name for *M. acuminata* subsp. *banksii* in Sāmoa is *lautaemanu*, which indicates spread via bird defaecation. The distance from the most easterly populations of *M. acuminata* subsp. *banksii* in New Guinea to Sāmoa is of a similar order to that required for long-distance dispersal from the most easterly occurring Fehi species/cultivars (in Makira and Choiseul, Solomon Islands) to Raʻiātea, Tahiti and the Marquesas (French Polynesia), viz. 5,000–7,000 km. Long-distance bird dispersal of seeds of many plant genera is also indicated between Pacific islands, and between Pacific islands and Indian Ocean islands, e.g., Carlquist (1967) and Harbaugh and Baldwin (2007).

Nadeaud (1873: 39) recorded that Fehi (as *M. feï*) was native in Tahiti, and that in December its fruits were full of well-developed and viable seeds (*ʻiriʻiri*). Naturalisation of Fehi in Tahiti is associated with:

1. Widespread cultivation of partly fertile Fehi cultivars, including the normally seedless *ʻaiori*, *ʻāʻata*, *tātiʻa* and possibly also *rūreva*, which bears seeded fruits under certain conditions, notably at higher elevations and during hot, dry periods (MacDaniels 1947: 14);
2. Presence of talus slopes—piles of loose, unstable rock formations that accumulate at the base of a cliff—which are well suited to colonisation and persistence by bananas, rather than by larger woody perennials (Simmonds 1959: 70);
3. Presence of Fehi fruit-consuming and seed-dispersing birds, including pigeons, large parrots and smaller parakeets, some of which survive but are highly endangered (Holyoak and Thibault 1984: 121–22; Kepler and Rust 2011: 256–57); and
4. Absence of competing plants which occupy similar niches elsewhere in the Pacific Islands, such as the wild *Musa*—and postulated parental species—in New Guinea and Solomon Islands, and a giant ginger (*Alpinia boia* Seem.) in Fiji.

The wild forms of Fehi in Tahiti and the Marquesas (Fig. 6) appear morphologically similar to cultivars in the ‘Aiori group. There are at least 11 informally named ‘Aiori cultivars in Tahiti (Kepler 2011; MacDaniels 1947: 23), briefly characterised as follows:

‘aiori mā‘a ‘ana‘ana	shining
‘aiori mā‘a piripiri	tight bunch, a bit sticky, tall
‘aiori mā‘a rahi	large fruit
‘aiori mā‘a āteatea	not tightly clustered
‘aiori mā‘a hu‘a	small fruit
‘aiori mā‘a menemene	fruit round/spherical
‘aiori mā‘a tāti‘a	tightly packed cluster
‘aiori mā‘a tanotano	fruit not widely spaced/not too tight, very smooth skin
‘aiori mā‘a varavara	hands wide apart
‘a‘ai‘a/*‘ārutu* (*teravero*)	1 (or 2) small leaves close to the bunch, attached approx. 2.5 cm below the basal bract inflorescence; larger fruits than *‘aiori*, basal fruits 18 × 15.5 cm; upper fruits more rounded with blunter apex

Polynesian native parakeets (*Vini* spp.) are nectivorous and are well known to feed on banana flowers, e.g., the critically endangered ultramarine lorikeet (*Vini ultramarina* Kuhl) feeds on Fehi flowers in the Marquesas (Thibault and Cibois 2017). Accordingly, the variation in ‘Aiori cultivars in Tahiti and the Marquesas could have arisen from genetic recombination associated with sexual reproduction as well as somatic variation, followed by their selection and maintenance by Fehi growers.

There is a sense of urgency in finding viable seeds and in assessing the taxonomic and conservation status of wild Fehi in Tahiti and the Marquesas, given threats from cattle and feral pig populations, environmentally invasive and ecosystem-transformative plant species such as *Miconia calvescens* DC. (Whittaker and Fernández-Palacios 2006: 318) and the banana corm weevil[30] (Kepler and Rust 2011: 444–50; Simmonds 1959: 68–70), historical unsustainable harvesting and management of wild stands (MacDaniels 1947: 10–11), bunchy top virus and climate change.

CONSERVATION, MANAGEMENT, USE AND IMPROVEMENT OF FEHI CULTIVARS

Throughout their cultivated ranges in the Pacific Islands, Fehi cultivars are disappearing and/or have been displaced by bananas of sect. *Musa*. This is due to a combination of factors:

1. They have lower palatability and sweetness, and an unpleasant acridity—unless fully ripe/overripe, with black skin and soft flesh, and/or cooked—by comparison with other banana cultivars (Kepler and Rust 2011: 259), as well as Islander diets switching to consumption of imported processed foods (Englberger, Daniells, *et al.* 2018: 170).
2. They are difficult to establish from suckers by comparison with most sect. *Musa* cultivars, the latter being generally less demanding, quicker-growing, higher-yielding, more versatile and more reliable. In order to flourish, Fehi require deep planting, partial shade, wind protection, regular fertilisation (high potassium) and watering, and removal of competitive grasses.
3. They prefer very high rainfall environments, such as the mountainous interiors of Tahiti (3,500 mm per annum); Kaua'i, Hawai'i (>4,000 mm per annum); Pohnpei, Federated States of Micronesia (4,800 mm per annum); and Makira, Solomon Islands (4,750 mm per annum), coupled with excellent drainage.
4. Fehi are not as vigorous as many other edible bananas and are relatively slow in their development, taking at least two years to reach harvest from a planted sucker compared with one year to harvest for other bananas, which leads to low productivity over time.
5. Their characteristic of turning urine bright yellow or orange-red has been misinterpreted as being unhealthy (Englberger, Daniells, *et al.* 2018: 170, 173).
6. They are susceptible to certain banana pests and diseases, most notably banana corm weevils and banana bunchy top virus (https://www.promusa.org/Fei+bananas) and need fertile, well-watered and well-drained soils (MacDaniels 1947: 10–11).
7. They suffer from grazing animals (feral pigs) and invasive plant species (e.g., *Miconia calvescens*), especially in Tahiti (Englberger, Daniells, *et al.* 2018: 173; Kepler and Rust 2011: 257; MacDaniels 1947: 9).
8. Several cultivars can be cultivated or become naturalised only at high elevations (too dry and possibly also too hot at sea level, including on the west coast of Tahiti or in the Marquesas).

Our thesis, that the Fehi bananas are an assemblage of cultivars and hybrids of *M. maclayi s.l.*, has important ramifications for their conservation and management. Firstly, it is vital that—notwithstanding biosecurity regulation challenges—the apparently great diversity in *M. maclayi* and related wild taxa be conserved *ex situ*, both in field gene banks and in tissue culture (at the International Musa Germplasm Collection, Leuven, Belgium, and the Pacific Community's Centre for Pacific Crops and Trees/SPC-CePACT, Suva, Fiji). There is an associated pressing need for better characterisation of the diversity in Fehi wild relatives, especially in Papua New Guinea, Bougainville and the Solomon Islands. In these areas, there is also a great need for ethnobiological studies of how local farmers manage the extraordinary biodiversity of wild and cultivated Musaceae and their interrelationships.

It is equally vital that selected cultivars/clones of Fehi be conserved *ex situ* in tissue culture and in field gene banks, notably in the field banana collection in Tahiti, French Polynesia. In addition to diverse Pacific plantains (Kagy *et al.* 2016), the Tahitian collection also conserves the diversity of Fehi cultivars from six different islands in French Polynesia and several Fehi cultivars from Papua New Guinea. It is strongly recommended that the Tahitian field banana collection be broadened to include Fehi cultivars from other Pacific nations using virus-indexed materials, most notably cultivars that have been developed in the Federated States of Micronesia, Bougainville and Solomon Islands (especially Makira), but also Vanuatu, Fiji, Sāmoa and eastern Indonesia, several of which are now at risk of extinction. It is also recommended that the Tahitian and other field collections be backed up in the International Musa Germplasm Transit Centre (ITC; Leuven, Belgium) and SPC Centre for Pacific Crops and Trees (CePACT; Suva, Fiji), and Fehi cultivars in *in vitro* collections be duplicated in field plantings (as much as resources will allow). All *Musa* materials entering ITC are tested against pests and diseases, including viruses, and cleaned from them when necessary, making it the ideal place to first send material, before re-sending it to other collections and/or repatriating to the supplier country.

It is also essential that selected cultivars/clones of Fehi be conserved *circa situ* by Pacific Islands communities and families and they be assisted to conserve their traditional Fehi cultivars in well-managed and effectively monitored traditional agroforestry systems. This will need to be coupled with the promotion of Fehi products in local and export markets, including value-added products such as provitamin A–rich, gluten-free flour and crisps. Lastly, the urgent need for further fieldwork on all aspects of these bananas underlines the importance of such work continuing to be interdisciplinary, with a strong local base.

CONCLUDING REMARKS

The diverse Fehi banana cultivars represent an underused, naturally highly nutritious food source for Pacific Islanders and others in the humid tropics. Along with other traditional Pacific crops, including sect. *Musa* cultivars, breadfruit and *Canarium* nut, Fehi bananas provide an agriculturally low-input, carbon-friendly source of carbohydrates and micronutrients. The early East Polynesian settlers were evidently observant and adept horticulturists who were able to select and vegetatively propagate new and useful cultivars of priority food and cultural plants from a limited number of original introductions, e.g., more than 20 named Fehi cultivars in Tahiti from four or five ancestral sources.

The patterns of Fehi cultivar diversity in the Pacific Islands bear similarities to those of two other important Polynesian canoe plants: breadfruit (*Artocarpus altilis* and relatives) and paper mulberry (*Broussonetia papyrifera*). Our findings have important implications for the history of human–plant interactions and movement in the Pacific Islands.

It is concluded that:

1. Fehi cultivars were likely first domesticated more than 3500 BP in Papuasia—especially northern New Guinea and Bismarck Archipelago—and in Lapita-associated movements, several early Fehi founder clones were dispersed southeast to Vanuatu, New Caledonia, Fiji and Sāmoa and north to Micronesia.[31]
2. On the basis of morphological and genetic data, the progenitor sources of eastern Polynesian cultivars of Fehi banana (and those of breadfruit and paper mulberry[32]) originated from Papuasia, with some passing through Micronesia rather than from central-western Polynesia (including Sāmoa), which has until recently been considered the likely source of East Polynesian canoe plants (e.g., Kirch and Green 2001). This more recent—ca. 900–1000 BP— eastward spread of Fehi founder clones is postulated to have begun from around the Solomon Islands (possibly Makira), reaching eastern Polynesia (the Marquesas and Tahiti) and, later, the Cook Islands and Hawai‘i, in accordance with the East Polynesian settlement hypothesis of Wilson (1985, 2012, 2018, 2021).
3. Linguistic studies also provide support that the source from which these plants reached East Polynesia was not Sāmoa but was instead centred in Polynesian Outliers in the southeast Solomons, with the closest major Solomon Island being San Cristobal/Makira.

Fehi have hitherto been comparatively neglected by *Musa* researchers, in part due to their challenging genomic makeup, different to commercial bananas. This review of Fehi cultivar variation provides a foundation for their further improvement and use, and for much-needed further interdisciplinary research.

ACKNOWLEDGEMENTS

We acknowledge the many Pacific Islanders, including informants in Indonesia and PNG, and researchers who supplied vital knowledge and images: these included Dr Mike Bourke, Dr Carol Lentfer, Dr Malcolm Ross, Dr Christopher Ballard and Kron Aken (Canberra, Australia); Dr Jaroslav Doležel (Czech Republic); Joseph Brider, Celine Dyer and William Wigmore (Cook Islands); Lois Englberger (Federated States of Micronesia); John and Harieta Bennett and Lili Tigarea (Rotuma, Fiji); Dr Richard Markham and Prof. Randy Thaman (Fiji); Julien Drouin (New Caledonia); Poi Okesene (Niue); Valerie Tuia (Samoa); Moses Pelomo (Solomon Islands); Dr Vincent Lebot and Fabien Cormier (Vanuatu); Forest and Kim Starr, Christopher Carter (USA); and linguists Dr Jacques Vernaudon (French Polynesia), Dr Laurie Reid (Japan), Dr Hsiu-chuan Liao (Taiwan), Dr David Kamholz (Berkeley, USA) and Dr Ken Rehg (Hawai‘i). We are most grateful to Max Ruas (Alliance Bioversity-CIAT, Montpellier, France) for his excellent assistance with generating the map.

REFERENCES

Académie Tahitienne | Fare Vāna‘a, 2017. *Dictionnaire tahitien–français | Fa‘atoro parau reo tahiti–reo farāni*. Pape‘ete: Fare Vāna‘a.

Argent, George C.G., 1976. The wild bananas of Papua New Guinea. *Notes from the Royal Botanic Garden, Edinburgh* 35 (1): 77–114.

Arnaud, Elizabeth and Jean-Pierre Horry (eds), 1997. *Musalogue: A Catalogue of Musa Germplasm: Papua New Guinea Collecting Missions 1988–1989*. Montpellier: International Network for the Improvement of Banana and Plantain.

Baker, John G., 1893. A synopsis of the genera and species of Museae. *Annals of Botany* 7 (26): 189–229.

Ballard, Chris, Paula Brown, R. Michael Bourke and Tracy Harwood (eds), 2005. *The Sweet Potato in Oceania: A Reappraisal.* Ethnology Monographs 19, Oceania Monograph 56. University of Pittsburgh and University of Sydney.

Barrau, Jacques, 1959. Sur l'origine et la distribution du bananier Fehi *Musa troglodytarum* L. *Études Mélanésiennes* 12–13: 45–49.

Bataillon, Pierre M., 1932. *Langue d'Uvea (Wallis): Grammaire-dictionnaire uvea–français, dictionnaire français–uvea–anglais*. Paris: Paul Geuthner.

Bedford, Stuart, Matthew Spriggs, David V. Burley, Christophe Sand, Peter Sheppard and Glenn R. Summerhayes, 2019. Debating Lapita: Distribution, chronology and subsistence. In S. Bedford and M. Spriggs (eds), *Debating Lapita: Distribution, Chronology and Subsistence*. Terra Australis 52. Canberra: Australian National University Press, pp. 5–33.

Blust, Robert, 1984–1985. The Austronesian homeland: A linguistic perspective. *Asian Perspectives* 26 (1): 45–67.

——2010. Malaita-Micronesian once again. *Oceanic Linguistics* 49: 559–67.

Brown, Forest B.H., 1931. *Flora of Southeastern Polynesia. 1. Monocotyledons.* Bernice P. Bishop Museum Bulletin 84, Bayard Dominick Expedition, Publ. No. 20, Honolulu.

Brucato, Nicolas, Mathilde André, Roxanne Tsang, Lauri Saag, Jason Kariwiga, Kylie Sesuki, Teppsy Beni, *et al*., 2021. Papua New Guinean genomes reveal the complex settlement of north Sahul. *Molecular Biology and Evolution* 38 (11): 5107–21. https://doi.org/10.1093/molbev/msab238

Burgos-Hernández, Mireya, Carmen Pozo and Dolores González, 2019. Evolutionary history of Musaceae: Ancient distribution and the rise of modern lineages. *Botanical Journal of the Linnean Society* 189: 23–35.

Carlquist, Sherwin, 1967. The biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. *Bulletin of the Torrey Botanical Club* 94 (3): 129–62.

Carreel, Françoise, Diego Gonzalez de Leon, Pierre Lagoda, Claire Lanaud, Christophe Jenny, Jean-Pierre Horry and Hugues Tézenas du Montcel, 2002. Ascertaining maternal and paternal lineage within *Musa* by chloroplast and mitochondrial DNA RFLP analyses. *Genome* 45 (4): 679–92.

Cenci, Alberto, Julie Sardos, Yann Hueber, Guillaume Martin, Catherine Breton, Nicolas Roux, Rony Swennen, Sebastien Christian Charpentier and Mathieu Rouard, 2021. Unravelling the complex story of intergenomic recombination in ABB allotriploid bananas. *Annals of Botany* 127 (1): 7–20.

Cheesman, Ernest E., 1947. Classification of the bananas: I. The genus *Ensete* Horan; II. The genus *Musa* L. *Kew Bulletin* 2 (2): 97–117.

——1949. Classification of the bananas: Critical notes on species: *Musa fehi*. *Kew Bulletin* 4 (4): 445–49.

Christelová, Pavla, Edmond De Langhe, Eva Hřibová, Jana Čížková, Julie Sardos, Markéta Hušáková, Ines Van den Houwe, *et al*., 2017. Molecular and cytological characterization of the global *Musa* germplasm collection provides insights into the treasure of banana diversity. *Biodiversity and Conservation* 26: 801–24.

Christenhusz, Maarten J.M., 2009. Typification of ornamental plants: *Musa textilis* (Musaceae). *Phytotaxa* 2: 53–54.

Christian, Frederick W., 1898. Nuku-oro vocabulary. *Journal of the Polynesian Society* 7 (4): 224–32.

Churchward, C. Maxwell, 1959. *Tongan Dictionary*. London: Oxford University Press.

Čížková, Jana, Eva Hřibová, Pavla Christelová, Ines Van den Houwe, Markku Häkkinen, Nicolas Roux, Rony Swennen and Jaroslav Doležel, 2015. Molecular and cytogenetic characterization of wild *Musa* species. *PLoS ONE* 10 (8): e0134096. https://doi.org/10.1371/journal.pone.0134096

Cormier, Fabien, 2010. *Catalogue of Musa Germplasm: The Vanuatu Banana Collection March 2010–September 2010*. Montpellier: International Centre of Advanced Agricultural Science and Rural Management.

Crook, William P., 2007. *An Account of the Marquesas Islands 1797–1799*. Tahiti: Éditions Haere Pō.

Cuzent, Gilbert, 1857. De la sève colorée du Fei. *Le Message de Tahiti*, March 1857.

Daniells, Jeff, 1990. The banana varieties of Tonga, Western Samoa and the Cook Islands. *Musarama* 3 (1): 6–10.

——1995. *Illustrated Guide to the Identification of Banana Varieties in the South Pacific*. Canberra: ACIAR Monograph No. 33, 43 pp.

——2007. *Consultancy Report on Characterization of Banana Varieties in Two Collections on Makira, Solomon Islands*. SPC/French Pacific Fund.

Daniells, Jeff, Lois Englberger and Adelino Lorens, 2004. *Pohnpei Banana Varieties—a Work in Progress*. 47 pp. Musalit.

——2011. Farm and forestry marketing profile for banana and plantain (*Musa* spp.). In C.R. Elevitch (ed.), *Speciality Crops for Pacific Island Agroforestry*. Hōlualoa, Hawai‘i: Permanent Agricultural Resources (PAR). https://agroforestry.net/scps

Daniells, Jeff and Steven B. Janssens, 2021. Identifying and classifying banana cultivars. In G. Kema and A. Drenth (eds), *Achieving Sustainable Cultivation of Bananas.* Vol. 2: *Germplasm and Genetic Improvement*. Cambridge, UK: Burleigh Dodds Science Publishing Limited, pp. 59–80.

Daniells, Jeff and Janet Paofa, 2007. Manus Island Banana Varieties—a Work in Progress. Unpublished manuscript, 54 pp.

Daniells, Jeff, Gabriel Sachter-Smith and Mary Taylor, 2016. Bananas adrift in time—a case study in the Solomons. *Acta Horticulturae* 1114: 27–32. https://doi.org/10.17660/ActaHortic.2016.1114.4

Daniells Jeff, Suzanne Sharrock and Rosa Kambuou, 1988. Report on the Second IBPGR/QDPI Banana Germplasm Collecting Mission to Papua New Guinea, 22 October to 27 November 1988. Musalit.

Davey, Mark W., Raganath Gudimella, Jennifer Ann Harikrishna, Lee Wan Sin, Norzulaani Khalid and Johan Keulemans, 2013. A draft *Musa balbisiana* genome sequence for molecular genetics in polyploid, inter- and intra-specific *Musa* hybrids. *BMC Genomics* 14: 683. https://doi.org/10.1186/1471-2164-14-683

De Langhe, Edmond, 2009. Relevance of banana seeds in archaeology. *Ethnobotany Research and Applications* 7: 271–81.

De Langhe, Edmond, Xavier Perrier, Mark Donohue and Tim P. Denham, 2015. The original banana split: Multi-disciplinary implications of the generation of African and Pacific plantains in Island Southeast Asia. *Ethnobotany Research and Applications* 14: 299–312.

De Langhe, Edmond, Luc Vrydaghs, Pierre de Maret, Xavier Perrier and Tim Denham, 2009. Why bananas matter: An introduction to the history of banana domestication. *Ethnobotany Research and Applications* 7: 165–77.

Dodds, Kenneth S., 1946. *Musa Fehi*, the indigenous banana of Fiji. *Nature* 157: 729–30. https://doi.org/10.1038/157729c0

Donohue, Mark and Tim P. Denham, 2009. Banana (*Musa* spp.) domestication in the Asia-Pacific region: Linguistic and archaeological perspectives. *Ethnobotany Research and Applications* 7: 293–332.

Dordillon, René I., 1999. *Grammaire et dictionnaire de la langue des îles Marquises 1904*. Tahiti: Société des Études Océaniennes.

Dwivany, Fenny M., Giasintha Stefani, Agus Sutanto, Husna Nugrahapraja, Ketut Wikantika, Adriana Hiariej, Topik Hidayat, *et al.,* 2020. Genetic relationship between Tongka Langit bananas (*Musa troglodytarum* L.) from Galunggung and Maluku, Indonesia, based on ITS2. *Hayati Journal of Biosciences* 27 (3): 258–65.

Edison, H.S., Agus Sutanto, Catur Hermanto, Hayati Lakuy and Yuliana Rumsarwir, 2002. *The Exploration of Musaceae in Irian Jaya (Papua). 11 February–5 March 2002*. Solok, Indonesia: Research Institute for Fruits.

Elbert, Samuel H., 1975. *Dictionary of the Language of Rennell and Bellona. Part 1. Rennellese and Bellonese to English*. Copenhagen: National Museum of Denmark.

——1988. *Echo of a Culture: Grammar of Rennell and Bellona*. Honolulu: University of Hawaii Press.

Englberger, Lois, Jeff Daniells, Adelino Lorens, Anne Vezina, Charlotte Lusty and Angela Kay Kepler, 2018. *Musa troglodytarum* (fe'i). In L.A.J. Thomson, J.C. Doran and B. Clarke (eds), *Trees for Life in Oceania: Conservation and Utilisation of Genetic Diversity*. Canberra: ACIAR, pp. 170–74.

Englberger, Lois, Ian Darnton-Hill, Terry Coyne, Maureen H. Fitzgerald and Geoffrey C. Marks, 2003. Carotenoid-rich bananas: A potential food source for alleviating vitamin A deficiency. *Food and Nutrition Bulletin* 24 (4): 303–18.

Englberger, Lois, Graham Lyons, Wendy Foley, Jeff Daniells, William G.L. Aalbersberg, Usaia Dolodolotawake, Claudine Watoto, *et al.*, 2010. Carotenoid and riboflavin content of banana cultivars from Makira, Solomon Islands. *Journal of Food Composition and Analysis* 23 (6): 624–32.

Fu, Ning, Meiyuan Ji, Mathieu Rouard, Hai-Fei Yan and Xue-Jun Ge, 2022. Comparative plastome analysis of Musaceae and new insights into phylogenetic relationships. *BMC Genomics* 23: 223. https://doi.org/10.1186/s12864-022-08454-3

Geraghty, Paul, 2009. Words of Eastern Polynesia: Is there lexical evidence for the origin of the East Polynesians? In A. Pawley and A. Adelaar (eds), *Austronesian Historical Linguistics and Culture History: A Festschrift for Robert Blust*. Canberra: Pacific Linguistics, pp. 445–60.

Grant, Martin L. 1930–1931. Journal in the Society Islands. Unpublished manuscript. Compiled by Dorothy Grant in May 1896.

Guild, Eastham, 1938. Tahitian aviculture: Acclimation of foreign birds. *Avicultural Magazine* 3: 8–11.

Häkkinen, Markku, 2013. Reappraisal of sectional taxonomy in *Musa* (Musaceae). *Taxon* 62: 809–13.

Häkkinen, Markku and Henry Väre, 2008. Typification and check-list of *Musa* L. names (Musaceae) with nomenclatural notes. *Adansonia*, Series 3, 30: 63–112.

Häkkinen, Markku, Henry Väre and Maarten J.M. Christenhusz, 2012. Identity of a *Pisang*—historical concepts of *Musa* (Musaceae) and the reinstatement of *Musa troglodytarum*. *Folia Malaysiana* 13 (2): 1–14.

Harbaugh, Danica T. and Bruce G. Baldwin, 2007. Phylogeny and biogeography of the sandalwoods (*Santalum*, Santalaceae): Repeated dispersals throughout the Pacific. *American Journal of Botany* 94 (6): 1028–40.

Henry, Teuira, 1928. *Ancient Tahiti*. Bernice P. Bishop Museum Bulletin 48, Honolulu.

Hermanto, Catur, Agus Sutanto, H.S. Edison, Riska Amril, Evert Hosang, Jeff Daniells and Yusdar Hilman, 2014. *Triangle Banana Exploration Report, Central Maluku and Lesser Sunda Islands, Indonesia. 16 February–6 March 2013*. Montpellier: Bioversity International. 18 pp.

Heslop-Harrison, J.S. and Trude Schwarzacher, 2007. Domestication, genomics and the future for banana. *Annals of Botany* 100 (5): 1073–84.

Hiariej, Adriana, Estri L. Arumingtyas, Wahyu Widoretno and Rodiyati Azrianingsih, 2015. Phenotypic variation of Fei banana (*Musa troglodytarum* L.) originated from Maluku islands. *Research Journal of Pharmaceutical, Biological and Chemical Sciences* 6 (2): 652–58.

Hill, Walter, 1874. *Report on the Brisbane Botanic Garden*: 7. Brisbane: James C. Beal.

Holyoak, David T. and Jean-Claude Thibault, 1984. Contribution à l'étude des oiseaux de Polynésie orientale. *Mémoires du Muséum national d'Histoire naturelle Série A, Zoologie*, tome 127. Paris: Muséum National d'Histoire Naturelle.

Janssens, Steven B., Filip Vandelook, Edmond De Langhe, Brecht Verstraete, Erik Smets, Ines Vandenhouwe and Rony Swennen, 2016. Evolutionary dynamics and biogeography of Musaceae reveal a correlation between the diversification of the banana family and the geological and climatic history of Southeast Asia. *New Phytologist* 210 (4): 1453–65. https://doi.org/10.1111/nph.13856

Jarret, Robert L., Nicholas Gawel, Alan Whittemore and Suzanne Sharrock, 1992. RFLP-based phylogeny of *Musa* species in Papua New Guinea. *Theoretical and Applied Genetics* 84 (5–6): 579–84.

Jouan, Henri, 1865. Recherches sur l'origine et la provenance de certains végétaux phanérogames observés dans les *îles* du Grand-Océan. Extrait des *Mémoires de la Société impériale des sciences naturelles de Cherbourg*, tome 11 : 1–98.

Kagy, Valérie, 1998. Importance culturelle et socio-économique de la banane dans la société Kanak en Nouvelle-Calédonie. Stage d'intégration dans la Fonction Publique territoriale au titre de l'article 83. Convention de stage no 98-83T-03. La Foa: CIRAD-FLHOR, 40 pp.

Kagy, Valérie and Françoise Carreel, 2004. Bananas in New Caledonian Kanak society: Their socio-cultural value in relation with their origins. *Ethnobotany Research and Applications* 2: 29–35.

Kagy, Valérie, Maurice Wong, Henri Vandenbroucke, Christophe Jenny, Cécile Dubois, Anthony Ollivier, Céline Cardi, *et al*., 2016. Traditional banana diversity in Oceania: An endangered heritage. *PLoS ONE* 11 (3): e0151208. https://doi.org/10.1371/journal.pone.0151208

Kallow, Simon, Kevin Longin, Natalia F. Sleziak, Steven B. Janssens, Filip Vandelook, John Dickie, Rony Swennen, Janet Paofa, Sebastien Charpentier and Bart Panis, 2020. Challenges for ex situ conservation of wild bananas: Seeds collected in Papua New Guinea have variable levels of desiccation tolerance. *Plants* 9 (9): 1243. https://doi.org/10.3390/plants9091243

Kennedy, Jean, 2008. Pacific bananas: Complex origins, multiple dispersals? *Asian Perspectives* 47 (1): 75–94. https://doi.org/10.1353/asi.2008.0004

——2009a. Bananas: Towards a revised prehistory. In A.S. Fairbairn and E. Weiss (eds), *From Foragers to Farmers: Papers in Honour of Gordon C. Hillman.* Oxford: Oxbow, pp. 190–204.

——2009b. Bananas and people in the homeland of genus *Musa*: Not just pretty fruit. *Ethnobotany Research and Applications* 7: 179–97.

Kennedy, Jean and William Clarke, 2004. *Cultivated Landscapes of the Southwest Pacific*. Resource Management in Asia-Pacific Working Paper No. 50. Canberra: Research School of Pacific and Asian Studies, Australian National University, pp. 1–47.

Kepler, Angela K., 2011. Tentative Attempts at Fē'ī Classification. Unpublished Powerpoint presentation to Global Musa Genetic Resources Network (MusaNet) Strategic Meeting, 28 February–3 March 2011, Montpellier, France.

Kepler, Angela K. and Francis G. Rust, 2011. *The World of Bananas in Hawai'i: Then and Now*. Hawai'i: Pali-O-Waipi'o Press.

Kirch, Patrick V., 1978. Indigenous agriculture on Uvea (Western Polynesia). *Economic Botany* 32 (2): 157–81.

——1997. *The Lapita Peoples: Ancestors of the Oceanic World*. Cambridge, MA: Blackwell.

Kirch, Patrick V. and Roger C. Green, 2001. *Hawaiki, Ancestral Polynesia: An Essay in Historical Anthropology*. Cambridge: Cambridge University Press.

Langdon, Robert, 1989. The significance of cultivated plant names in the settlement of East Polynesia. In R. Harlow and R. Hooper (eds), *VICAL 1, Oceanic Languages: Papers from the Fifth International Conference on Austronesian Languages*. Auckland: Linguistic Society of New Zealand, pp. 305–33.

Lasalita-Zapico, Florence C., Catherine Hazel M. Aguilar and J.M. Aujero, 2010. Phenotypic variability of Manila hemp (*Musa textilis* L. Nee) genotypes in southern Mindanao Island, Philippines. *Journal of Tropical Agriculture* 48 (2): 68–70.

Lebot, Vincent, 1999. Biomolecular evidence for plant domestication in Sahul. *Genetic Resources and Crop Evolution* 46: 619–28.

Lebot, Vincent, Malli Aradhya, Richard M. Manshardt and Brien Meilleur, 1993. Genetic relationships among cultivated bananas and plantains from Asia and the Pacific. *Euphytica* 67: 163–75.

Lentfer, Carol J., 2009. Tracing domestication and cultivation of bananas from phytoliths: An update from Papua New Guinea. *Ethnobotany Research and Applications* 7: 247–70.

Lentfer, Carol J., Alison Crowther and Roger C. Green, 2021. The question of early Lapita settlements in Remote Oceania and reliance on horticulture revisited: New evidence from plant microfossil studies at Reef/Santa Cruz, south-east Solomon Islands. *Technical Reports of the Australian Museum Online* 34: 87–106. https://doi.org/10.3853/j.1835-4211.34.2021.1745

Lentfer, Carol J., Christina Pavlides and Jim Specht, 2010. Natural and human impacts in a 35 000-year vegetation history in central New Britain, Papua New Guinea. *Quaternary Science Reviews* 29: 3750–67.

Lipson, Mark, Pontus Skoglund, Matthew Spriggs, Frédérique Valentin, Stuart Bedford, Richard Shing, Hallie Buckley, *et al.*, 2018. Population turnover in Remote Oceania shortly after initial settlement. *Current Biology* 28 (7): 1157–65.

Liu, Yue-Chen, Rosalind Hunter-Anderson, Olivia Cheronet, Joanne Eakin, Frank Camacho, Michael Pietrusewsky, Nadin Rohland, *et al*., 2022. Ancient DNA reveals five streams of migration into Micronesia and matrilocality in early Pacific seafarers. *Science* 377: 72–79. https://doi.org/10.1126/science.abm6536

MacDaniels, Laurence H., 1947. *A Study of the Feʻi Banana and Its Distribution with Reference to Polynesian Migrations*. Bernice P. Bishop Museum Bulletin 190, Honolulu, 1–56 pp.

Matthews, Peter J., 2014. *On the Trail of Taro: An Exploration of Natural and Cultural History*. Senri Ethnological Studies 88. Osaka: National Museum of Ethnology.

McClatchey, Will, Randy R. Thaman and Saula Vodonaivalu, 2000. A preliminary checklist of the flora of Rotuma with Rotuman names. *Pacific Science* 54 (4): 345–63.

Merrill, Elmer D., 1917. *An Interpretation of Rumphius's Herbarium Amboinense*. Manila: Bureau of Printing.

Mueller, Ferdinand J.H. von, 1875. Musaceae. *Fragmenta Phytographiæ Australiæ* 9: 188–90.

——1885. Appendix: Edible fruits from the Maclay-Coast, New Guinea. *Proceedings of the Linnean Society of New South Wales* 10: 355–58.

Nadeaud, Jean, 1873. *Énumération des plantes indigènes de l'île de Tahiti*. Paris: F. Savy.

Noyer, Jean-Louis, Sandrine Causse, Kodjo Tomekpe, André Bouet and Franc-Christophe Baurens, 2005. A new image of plantain diversity assessed by SSR, AFLP and MSAP markers. *Genetica* 124: 61–69.

Pedro, Nicole, Nicolas Brucato, Veronica Fernandes, Mathilde André, Lauri Saag, William Pomat, Céline Besse, *et al.*, 2020. Papuan mitochondrial genomes and the settlement of Sahul. *Journal of Human Genetics* 65: 875–887. https://doi.org/10.1038/s10038-020-0781-3

Perrier, Xavier, Frédéric Bakry, Françoise Carreel, Christophe Jenny, Jean-Pierre Horry, Vincent Lebot and Isabelle Hippolyte, 2009. Combining biological approaches to shed light on the evolution of edible bananas. *Ethnobotany Research and Applications* 7: 199–216.

Perrier, Xavier, Edmond De Langhe, Mark Donohue, Carol J. Lentfer, Luc Vrydaghs, Frédéric Bakry, Françoise Carreel, *et al.*, 2011. Multidisciplinary perspectives on banana (*Musa* spp.) domestication. *Proceedings of the National Academy of Sciences (PNAS)* 108 (28): 11311–18.

Perrier, Xavier, Christophe Jenny, Frédéric Bakry, Deborah Karamura, Mercy Kitavi, Cécile Dubois, Catherine Hervouet, Gérard Philippson and Edmond De Langhe, 2019. East African diploid and triploid bananas: A genetic complex transported from South-East Asia. *Annals of Botany* 123 (1): 19–36.

Ploetz, Randy C., Angela K. Kepler, Jeff Daniells and Scot C. Nelson, 2007. Banana and plantain—an overview with emphasis on Pacific Islands: Musaceae (banana family). In C.R. Elevitch (ed.), *Species Profiles for Pacific Island Agroforestry* (series). Hōlualoa, Hawai'i: Permanent Agriculture Resources, 27 pp.

Posth, Cosimo, Kathrin Nägele, Heidi Colleran, Frédérique Valentin, Stuart Bedford, Kaitip W. Kami, Richard Shing, *et al.*, 2018. Language continuity despite population replacement in Remote Oceania. *Nature Ecology and Evolution* 2: 731–40.

Rant, A., 1934. Twee botanische reizen naar Ambon. *Natuurkundig Tijdschrift Nederlandsch·lndie* 94: 100–133.

Rensch, Karl H., 1984. *Tikisionalio fakauvea–fakafalani | Dictionnaire wallisien–français*. Pacific Linguistics, Series C, No. 86. Canberra: Australian National University.

Ross, Malcolm, 2008. Staple foods: Root crops, bananas, breadfruit and sago. In M. Ross, A. Pawley and M. Osmond (eds), *The Lexicon of Proto Oceanic: The Culture and Environment of Ancestral Oceanic Society.* Vol. 3: *Plants*. Pacific Linguistics 599. Canberra: Research School of Pacific Studies, Australian National University, pp. 255–92.

Rumphius, Georg E., 1747. *Herbarium Amboinense.* Vol. 5. Amsterdam: François Changuion, Hermanus Uytwerf.

Sabatier, Ernest. 1971. *Gilbertese–English Dictionary*. Translated by Sister Oliva. Sydney: South Pacific Commission Publications Bureau.

Sachter-Smith, Gabriel L., 2011. Bananas of the Solomon Islands: A Catalog of the Banana Plants Seen in the Islands of Guadalcanal, Makira and Malaita. Report for Bioversity International and Global Crop Diversity Trust, 54 pp.

Sachter-Smith, Gabriel L., Janet Paofa, Gou Rouka, Julie Sardos and Steven Janssens, 2016. *Bananas of the Autonomous Region of Bougainville: A Catalog of Banana Diversity Seen on the Islands of Bougainville and Buka, Papua New Guinea*. Papua New Guinea NARI, Musanet & Bioversity International.

Sagot, Paul A., 1886. Bananier féhi, sa forme asperme et sa forme seminifère. *Bulletin de la Société Botanique de France* 33: 317–26.

——1893. *Manuel Pratique des Cultures Tropicales et des Plantations des Pays Chauds*. Edited by E. Raoul. Paris: Augustin Challamel.

Sardos, Julie, Catherine Breton, Xavier Perrier, Ines Van Den Houwe, Janet Paofa, Mathieu Rouard and Nicolas Roux, 2021. Wild to domesticates: Genomes of edible diploid bananas hold traces of several undefined genepools. bioRxiv preprint, posted 31 Jan. 2021. https://doi.org/10.1101/2021.01.29.428762

Sardos, Julie, Pavla Christelová, Jana Čížková, Janet Paofa, Gabriel L. Sachter-Smith, Steven B. Janssens, Gou B. Rauka, *et al.*, 2018. Collection of new diversity of wild and cultivated bananas (*Musa* spp.) in the Autonomous Region of Bougainville, Papua New Guinea. *Genetic Resources and Crop Evolution* 65: 2267–86. https://doi.org/10.1007/s10722-018-0690-x

Sardos, Julie, Janet Paofa, Gabriel L. Sachter-Smith, Ezra Togabalaguguwa, Eva Hribova, Ines Van den Houwe and Nicolas Roux, 2019. Report of the Banana Collecting Mission to the Province of West New Britain (WNB), Papua New Guinea, from September 30th to October 12th, 2019. Bioversity International/ CIAT Alliance and Papua New Guinea NARI.

Sardos, Julie, Mathieu Rouard, Yann Hueber, Alberto Cenci, Katie E. Hyma, Ines van den Houwe, Eva Hribova, Brigitte Courtois and Nicolas Roux, 2016. A genome-wide association study on the seedless phenotype in banana (*Musa* spp.) reveals the potential of a selected panel to detect candidate genes in a vegetatively propagated crop. *PLoS ONE* 11 (5): e0154448. https://doi.org/10.1371/journal.pone.0154448

Sardos, Julie, Gabriel L. Sachter-Smith, Michel E. Ghanem, Eva Hribova, Ines Van den Houwe, Nicolas Roux and William Wigmore, 2019. Report of the Banana Collecting Mission to Rarotonga and Aitutaki, Cook Islands, 20 May to 31 May, 2019. Technical Report to Bioversity International; Ministry of Agriculture, Govt. of Cook Islands and Pacific Community.

Sardos, Julie, Gabriel L. Sachter-Smith, Arshni Shandil, Ines Van den Houwe, Eva Hribova, Parate Matalavea, Anesone Vaai, Tolo Iosefa, David Tilafono Hunter and Nicolas Roux, 2019. Report of the Banana Collecting Mission to Samoa from July 22nd to August 2nd, 2019. Technical Report to Bioversity International/ CIAT Alliance; Ministry of Agriculture and Fisheries, Govt. of Samoa, and Pacific Community.

Seemann, Berthold, 1865. *Flora Vitiensis: A Description of the Plants of the Viti or Fiji Islands, with an Account of Their History, Uses and Properties.* Vol. 1. London: L. Reeve and Co.

Sharrock, Suzanne, 2001. Diversity in the genus *Musa*: Focus on Australimusa. In *Networking Banana and Plantain: INIBAP Annual Report 2000.* Montpellier: International Network for the Improvement of Banana and Plantain, pp. 14–19.

Sheppard, Peter, 2019. Early Lapita colonisation of Remote Oceania: An update on the leapfrog hypothesis. In S. Bedford and M. Spriggs (eds), *Debating Lapita: Distribution, Chronology and Subsistence.* Terra Australis 52. Canberra: Australian National University Press, pp. 135–54.

——2022. Southeast Solomon Islands in regional perspective: Settlement history, interaction spheres, Polynesian Outliers and eastward dispersals. *Journal of the Polynesian Society* 131 (2): 113–84. https://doi.org/10.15286/jps.131.2.113-184

Simmonds, Norman W., 1953. The development of the banana fruit. *Journal of Experimental Botany* 4 (1): 87–105. https://doi.org/10.1093/jxb/4.1.87

——1956. Botanical results of the banana collecting expedition 1954–5. *Kew Bulletin* 11: 463–89.

——1959. *Bananas (Tropical Agricultural Series)*. New York: Longman.

——1962. *The Evolution of the Bananas*. New York: Longman.

Simmonds, Norman W. and S.T. Colin Weatherup, 1990. Numerical taxonomy of the wild bananas (*Musa*). *New Phytologist* 115 (3): 567–71. https://doi.org/10.1111/j.1469-8137.1990.tb00485.x

Skoglund, Pontus, Cosimo Posth, Kendra Sirak, Matthew Spriggs, Frederique Valentin, Stuart Bedford, Geoffrey A. Clark, *et al.*, 2016. Genomic insights into the peopling of the Southwest Pacific. *Nature* 538: 510–13. https://doi.org/10.1038/nature19844

Smith, Albert C., 1979. *Flora Vitiensis Nova: A New Flora of Fiji (Spermatophytes Only).* Vol. 1. Kaua‘i, Hawai‘i: Pacific Tropical Botanical Garden.

Stover, Robert H. and Norman W. Simmonds, 1987. *Bananas.* 3rd edition. Burnt Mill, Harlow, UK: Longman Scientific and Technical.

Sutanto, Agus, H.S. Edison, Riska Amril, Fazli Nasution, Catur Hermanto, Jana Čížková, Eva Hřibová, *et al.*, 2016. Collecting banana diversity in eastern Indonesia. *Acta Horticulturae* 1114: 19–26. https://doi.org/10.17660/ActaHortic.2016.1114.3

Thibault, Jean-Claude and Alice Cibois, 2017. *Birds of Eastern Polynesia: A Biogeographic Atlas*. Barcelona: Lynx Edicions.

Vieillard, Eugène, 1862. Plantes utiles de la Nouvelle-Calédonie. *Annales des Sciences Naturelles*, 4th Series, Botanique, tome 16: 28–76.

Walter, Annie and Chanel Sam, 2002. *Fruits of Oceania*. Translated by P. Ferrar. Monograph No. 85. Canberra: ACIAR.

Waterhouse, J.H. Lawry, 1928. *A Roviana and English Dictionary*. Melanesian Mission Press.

Whistler, W. Arthur, 1984. Annotated list of Samoan plant names. *Economic Botany* 38 (4): 464–89.

——2000. *Plants in Samoan Culture: The Ethnobotany of Samoa*. Hawai‘i: Isle Botanica.

Whittaker, Robert J. and José María Fernández-Palacios, 2006. *Island Biogeography: Ecology, Evolution, and Conservation*. 2nd edition. Oxford: Oxford University Press.

Wilder, Gerrit P., 1931. *Flora of Rarotonga*. Bernice P. Bishop Museum Bulletin 86, Honolulu.

Wilson, William H., 1985. Evidence for an Outlier source for the Proto-Eastern Polynesian pronominal system. *Oceanic Linguistics* 24 (1/2): 85–133.

——2012. Whence the East Polynesians? Further linguistic evidence for a Northern Outlier source. *Oceanic Linguistics* 51: 289–359.

——2018. The Northern Outliers–East Polynesian hypothesis expanded. *Journal of the Polynesian Society* 127 (4): 389–423.

——2021. East Polynesian subgrouping and homeland implications within the Northern Outlier–East Polynesian Hypothesis. *Oceanic Linguistics* 60 (1): 37–72.

Yee, Warren, Ernest K. Akamine, George M. Aoki, Richard A. Hamilton, Frank H. Haramoto, Richard B. Hine, Oliver V. Holtzmann, *et al.*, 1970. *Papayas in Hawaii*. University of Hawaii Cooperative Extension Service Circular 436.

Yen, Douglas E., 1974a. Arboriculture in the subsistence of Santa Cruz, Solomon Islands. *Economic Botany* 28 (3): 247–84.

——1974b. *The Sweet Potato and Oceania: An Essay in Ethnobotany*. Bernice P. Bishop Museum Monograph 236, Honolulu.

——1993. The origins of subsistence agriculture in Oceania and the potential for future tropical food crops. *Economic Botany* 47 (1): 3–14.

Yuncker, Truman G., 1943. *The Flora of Niue Island*. Bernice P. Bishop Museum Bulletin 178, Honolulu.

Zerega, Nyree, Diane Ragone and Timothy J. Motley, 2006. Breadfruit origins, diversity, and human-facilitated distribution. In T.J. Motley, N. Zerega and H. Cross (eds), *Darwin's Harvest: New Approaches to the Origins, Evolution, and Conservation of Crops*. New York: Columbia University Press, pp. 213–38.

AUTHOR CONTACT DETAILS

Lex A.J. Thomson, Australian Centre for Pacific Islands Research, Australia. University of the Sunshine Coast, Sippy Downs, QLD, Australia. lex.thomson@gmail.com | https://orcid.org/0000-0002-2984-0711

Jean-François Butaud, Tahiti, French Polynesia. jfbutaud@hotmail.com | https://orcid.org/0000-0002-8025-5526

Jeff Daniells, Queensland Department of Agriculture and Fisheries, Australia. Jeff.Daniells@daf.qld.gov.au

Paul A. Geraghty, University of the South Pacific, Fiji. paul.geraghty@usp.ac.fj | https://orcid.org/0000-0001-5574-7660

Adriana Hiariej, Universitas Pattimura, Seram, Indonesia. hiariejd@yahoo.com

Valérie Kagy, Institut agronomique néo-Calédonien, New Caledonia. valerie.kagy@iac.nc

Jean Kennedy, Australian National University, Australia. jean.kennedy@anu.edu.au

Angela K. Kepler, Hawai‘i, USA. akk@pacificwideconsulting.com

David J. Mabberley, Australian Institute for Botanical Science (National Herbarium of New South Wales), Sydney, Australia. david_mabberley@yahoo.co.uk

Gabriel L. Sachter-Smith, Hawai‘i, USA. gabe.sachter@gmail.com

Julie Sardos, Alliance Bioversity-CIAT, Montpellier, France. j.sardos@cgiar.org

William H. Wilson, University of Hawai‘i at Hilo, USA. wilsonwi@hawaii.edu | https://orcid.org/0000-0003-0296-6063

Maurice Wong, Direction de l'Agriculture, Tahiti, French Polynesia. maurice.wong@rural.gov.pf