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- to coordinate and support the collection and exchange of documentation and information related to these crops;
- to coordinate and support training for researchers and technicians from developing countries.



International Network for the Improvement of Banana and Plantain

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Réseau International pour l'Amélioration de la Banane et de la Banane Plantain
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Identification of genetic diversity in the genus *musa*

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OBSERVATIONS ON *MUSA* TAXONOMY

K. Shepherd

Undoubtedly there are still poorly defined or as yet unidentified taxa in the genus *Musa*. However, the existing taxonomy is comprehensive and substantially accurate enough as a taxonomist's tool to describe distinct forms and to put them into superficially sound groupings. I say 'superficially' because where taxonomy sometimes fails is in the poor correspondence between groupings (sections) and the cytogenetic evidence obtainable from inter-specific hybrids. In 1962, Simmonds discussed the evolution of bananas. The writer is now in a position to rectify and amplify Simmonds (1962) in several important respects.

THE SPECIES

With the exception of *M. ingens* (2n = 14), *M. beccarii* (2n = 18) and perhaps the mysterious *M. lasiocarpa*, all species studied so far have been classifiable into one of Cheesman's four sections (two each with 2n = 22 and 2n = 20). Of the few additions that have been made to Simmonds' listings (Simmonds, 1960; 1962) I am aware of the following:

- Meijer (1961) described certain species from Sumatra. Of particular interest was the small-seeded *M. halabanensis*, which the author once saw flowering in Trinidad. Meijer's *M. malaccensis* is elsewhere regarded as a subspecies of *M. acuminata* (confirmed by personal observation in the Bogor collection and by observation of an accession from Sumatra in the Bahia collection). Simmonds has also suggested that *M. sumatrana* is *M. acuminata*.
- Shepherd (1964) described a very small-seeded (*Eumusa* from India as *M. ochracea*.
- Argent (1976) distinguished a number of new taxa in section Australimusa from the New Guinea area. He also wished to separate *M. banksii* as a species, as opposed to a subspecies of *M. acuminata*, but on quite erroneous grounds.
- *M. hukuensis* was described in the 1970s, despite my positive earlier identification of the seeds, young plants and, later, of flowering plants, as a slightly aberrant *M. balbisiana*.

Two of the previous reports raise an important question. What is the basis for assigning a subspecific or a specific rank? Such a decision cannot properly be made by historical tracking of plant material from a single geographical area. Nor should it be attempted even after an extensive field trip. Such a decision should be delayed until more exhaustive and comparative studies can be made in a living collection with material from many areas, and where cytogenetic as well as morphological evidence can be considered.

Sections (*Eu-*) *Musa* and *Rhodochlamys* (2n = 22)

The separation of these two sections is a taxonomic convenience based on the fact that species of *Rhodochlamys* are smaller and bear erect inflorescences, typically with only a single row of flowers at each node. However, this distinction

between the sections does not reflect the relative reproductive isolation of the species. Such isolation can be weaker in inter-sectional crosses than in crosses within the same section, as the following three examples attempt to illustrate.

F₁ hybrids of *M. flaviflora* (*Eumusa*) and *M. ornata* (*Rhodochlamys*), obtained from crosses in either direction, are very vigorous and virtually 100% male and female fertile. Eleven pairs are regularly found at meiosis and there is no suggestion of inversion hybridity such as occurs when either species is crossed with a third one.

M. velutina (*Rhodochlamys*) is rather weakly isolated from either of the above. Both F₁ and backcross generations of *M. flaviflora* (F) × *M. velutina* (V) include many vigorous and fertile plants. Characteristics of some (F × V) × F plants seem to indicate that *M. ornata* is a secondary species derived from a natural hybrid swarm of these two.

M. laterita (*Rhodochlamys*) is quite sharply isolated from the other three species already mentioned. F₁ hybrids of the three combinations are sterile or nearly so. Yet, like *M. flaviflora* and *M. ornata* (the behavior of *M. velutina* is still uncertain), it can make appreciably male- and female-fertile hybrids with particular forms of *M. acuminata*. *M. laterita* and ssp. *burmannica* appear to share a common homozygous segmental translocation. It is known that highly vigorous and fertile plants may be selected in the F₂ and backcross generations of their hybrids.

Within *Eumusa*, *M. acuminata* can form male- and female-fertile hybrids with *M. schizocarpa* (New Guinea) and *M. ochracea* (India), as well as with *M. flaviflora*. Based on the characteristics of its inflorescence, *M. halabanensis* may also present a similar degree of affinity. Unfortunately, information is scarce on crosses between these allied species, or between them and *Rhodochlamys*, except in the case of *M. flaviflora*.

Estimates of reproductive isolation in certain other pairings have been clouded by the selection of only one or two accessions of *M. acuminata* and *M. balbisiana* and the possibly erroneous assumption that these are representative of the species. These two species are considered by Simmonds (1962) to be quite isolated from one another. However, in Brazil we have obtained normally female-fertile (yet male-sterile) hybrids between another form of *M. balbisiana* and subspecies *burmannica* and *banksii*. The level of fertility in the hybrids is not high. However, in backcrosses of the F₁ to *M. acuminata*, there is a percentage of vigorous and partially male-fertile plants.

There are certainly many species combinations to be tested and others that might be worth studying again. However, from the plant breeder's viewpoint the most interesting aspect is the possibility of gene transfer from other species to *M. acuminata*. In practice, this latter species would be the recurrent parent in a sequence of backcrosses. Success would depend on the simple inheritance of the characteristic to be transferred. The process would be time-consuming. In no case can the extent of natural introgression between *M. acuminata* and other species be estimated. Argent (1976) noted hybrids of *M. banksii* and *M. schizocarpa*. This is to be expected. However, their uniformity suggests that they were F₁ hybrids only, despite their partial male and female fertility.

Sections *Callimusa* and *Australimusa* (2n = 20)

On the evidence of the species hybrids studied, these two sections are of very different status. In the case of *Callimusa*, admittedly only two species were considered, *M. violascens* and *M. bornensis*. The hybrid between these species exhibited reduced chromosome pairing and much reduced fertility. The same was true of crosses between either of these species and forms of *Australimusa*. In contrast, crosses involving *M. textilis*, *M. lolodensis*, *M. pekelii*, *M. angustigena* and *M. maclayi* (*Australimusa*), commonly revealed high levels of chromosome pairing. Hybridity was occasionally observed for a single translocation and/or the presence of anaphase bridges. The accession of *M. lolodensis* evidently differed from the others by an inversion. The *Australimusa* hybrids are all moderately to abundantly fertile. It is surprising therefore that they maintain their identity in the New Guinea area. In Jamaica, we once received a batch of seeds from Buka, the plants from which were very suggestive of a hybrid swarm.

We conclude that *Australimusa* is quite a young group whose species are more geographic isolates than genetic ones, despite the morphological dissimilarities. A curious point is the evidence of a cline in seed size from *M. textilis* (native to Borneo?) to the largest-seeded taxa at the easterly end of the range. It might even be questioned whether the major taxa merit specific status or should be thought of as subspecies, as in the analogous case of *M. acuminata*.

In *Callimusa* we can conclude that at least two of the species are reproductively well-isolated from each other and from *Australimusa*. This suggests a much older differentiation.

Hybrids Between Sections of Unlike Chromosome Number

A small number of such hybrids have been experimentally produced. The female parent has always been a species with 2n = 22. The strangest example was perhaps the combination of *M. balbisanu* × *M. beccarii* (2n = 11 + 9 = 20). Bernardo's (1957) account of meiosis in such hybrids is in strong disagreement with studies made by Dodds and the author. In six different combinations with 2n = 21 or 20, we found about one pair or less at the first meiotic division. Sterility was complete.

TAXONOMY OF WILD *MUSA ACUMINATA*

Despite Meijer's (1961) and Argent's (1976) reports, the concept of subspecies within the diverse and wide-ranging species *M. acuminata*, is a very convenient one. As Simmonds (1962) noted, the variability is for the most part geographically discontinuous, although some introgression may have occurred and may now be occurring. The fertility of subspecies hybrids is, in some instances, limited by heterozygosity for chromosomal structural changes (primarily translocations), but evidently not by a lack of chromosomal homology. There is, on the whole, no doubt that, although some degree of F₂ breakdown may exist, the subspecies can interbreed readily when brought together naturally or experimentally.

Opinions may differ on the number of subspecies to be recognized and in the

definition of their ranges. However, in my view, the rank of subspecies should include the largest possible conglomerate of populations consistent with the cytological as well as the morphological evidence. For example, forms of the species from Sri Lanka, Madras and Burma are more striking for their similarities than for their differences. The separation of one part of the variability as ssp. *burnmannioides* is unjustified. The reference to 'Madras' refers to an accession in the Jamaican collection from that part of India which is very close to the old Botanic Garden accession 'Calcutta'.

I am not totally convinced of the validity of separating ssp. *siamea*, as limited below, from ssp. *burnmannia*. These subspecies have some common characteristics including their segmental translocations. My limitation of the range of ssp. *siamea* omits the North Malayan Kedah form included by Simmonds (1956). When seen in a collection alongside other subspecies, rather than in isolation, the Kedah form is clearly ssp. *malaccensis*. This judgement is reinforced by its chromosome structure. It would now seem, in fact, that ssp. *malaccensis* extends into South Thailand rather than ssp. *siamea* into Malaya. Meijer's (1961) identification of *M. malaccensis* in Sumatra is well confirmed by the specimens in the Cibinong (Bogor) collection and by an accession in Bahia from Jambi in Sumatra. Simmonds (1956) also erred in including *M. truncata* Ridley under ssp. *microcarpa*. The strongest evidence for its separation is that of its translocation structure (three changes relative to ssp. *microcarpa*). However, its appearance in a collection is distinctive. The highland *M. acuminata* from Malaya must be regarded as ssp. *truncata*.

I have not seen Paul Allen's description of ssp. *errans*, nor am I familiar with the plant, since accessions received in Jamaica died of Panama disease before flowering. How different is it from ssp. *banksii*?

The remaining large gaps in the subspecific taxonomy of *M. acuminata* occur in Indonesia. How different is *M. sumatrana* from ssp. *malaccensis*? Can all Javanese forms be included within subspecies *zebrina* although only some specimens are vividly pigmented? Can all the *M. acuminata* from Borneo be referred to as ssp. *microcarpa*? What forms exist in Sulawesi or in the islands between Sulawesi and New Guinea? The National Biological Institute in Bogor is known to be working on at least some of these problems and perhaps could benefit from support in organizing collections.

The plant populations in Pemba Island, Tanzania also remain unclassified. Accessions in Trinidad unfortunately did not survive. However, hybrids showed that they were separated by a distinctive segmental translocation from other material. Perhaps it will be useful to present here, in summary form, the likely subspecific framework of *M. acuminata*.

- *burnmannia* (to re-include ssp. *burnmannioides*). Range: Sri Lanka, eastern India (including Assam?), Burma, possibly encroaching on northwest Thailand and in some localities overlapping with the following
- *siamea*. Similar to the previous subspecies in chromosome structure and in certain morphological features. Range: southern (?), central, northern and eastern Thailand, Indo-China.
- *malaccensis*. Range: southern Thailand (perhaps introgressing with ssp. *siamea*), northern Malaya, where populations differ by a single chromosome translocation from Central Malayan ones, and also in Sumatra.

- *truncata*. Range: higher elevations in Malaya and perhaps southern Thailand.
- undefined (perhaps 2-3). Range: Sumatra, Java, Kalimantan and Sulawesi.
- *microcarpa*. Range: at present defined only from Sabah and Sarawak.
- *banksii*. Range: Irian Jaya, Papua New Guinea and Northeast Australia – also inexplicably in Samoa but not in Fiji or in any other intermediate island group.
- *errans*. Range: Philippines; perhaps to be compared with ssp. *banksii*.
- undefined. Range: confined to Tanzania?

Attention may be drawn to a current misunderstanding on ssp. *malaccensis* and ssp. *microcarpa*, "ces deux sous-espèces se côtoient dans une même zone (zone centrale définie par Shepherd)". This refers solely to the arrangement of chromosome arms where both of these subspecies, and also ssp. *banksii*, evidently display the ancestral structure. They are quite distinct in morphology.

THE SUBSPECIES AND THE CULTIVAR GROUPS

My position on this subject is simply stated. Although there are some obvious placements such as 'Pisang Lilin'/'Lidi' in ssp. *malaccensis*, I have never felt confident enough to attempt a general classification, even of the AA Group. I think that the classifications that have been constructed are a source of confusion and it is no surprise that discrepancies exist between different lists. As an example, in both the Philippine and the Honduran collections 'Pisang mas' is listed as a derivative of ssp. *microcarpa* which I cannot see at all.

'Pisang mas' ('Sucrier') is interesting in another respect. It is equal to Type 19 of Dodds (1943) who found it to be heterozygous for no fewer than three segmental translocations. This surely implies a hybrid origin. Of seven other AA cultivars, for which the results of meiotic investigations are available, only 'Sikuzani' is homozygous for translocation structure. In this case it is the structure of the North Malayan ssp. *malaccensis* which it little resembles. It may be noted that 'Pisang lilin' is heterozygous for this same translocation.

We can only speculate on the various origins of cultivated AA diploids, which are themselves basic to the evolution of the triploid cultivars. Based on their present distributions and synonymies, at least some have long been dispersed, with or without human migrations. How else could 'Pisang Mas' and 'P. Jari Buaya' be virtually ubiquitous in Southeast Asia? Also, the dispersal of diploid forms more fertile than these are now, implies the probability of their having intercrossed with cultivars and wild forms of other areas. This assumes that the AA Group, as it is now known, is composed predominantly of hybrids that, to judge from their experimental breeding behavior, are highly heterozygous. We should be very wary of attempting to associate plantains with the New Guinea diploids or of linking East African highland AAAs with any particular subspecies. I am understandably pleased that recent isozyme studies are leading to the same conclusions.

ADD AND BBB CULTIVARS

The morphological basis for this discrimination has not been published to my knowledge. If it is based on a subjective scoring of our 15 characters (Simmonds

and Shepherd, 1955), I would not be impressed. There are, in fact, two characters among the fifteen that can be taken as sure indicators of the presence of an A genome. The first of these is male bracts, which roll or fold back after lifting, even if sometimes rather weakly. I have never observed this character in any strain of *M. balbisiana*. The other characteristic is the presence of a corrugation found behind the tip of the male flower free tepals. Again, I have never seen this in *M. balbisiana*. The only verification I can offer at this time is a 'Saba' introduced into the Bahian collection from Honduras. It has the expected bunch appearance, similar to that of the numerous strange ABB cultivars in the Papua New Guinea collection. It also has bracts that fold and tend to curl as well as corrugated free tepals. However, 'Kluai Lep Chang Kut', seen at Pak Chong in Thailand, definitely lacks these A characteristics and must be accepted as BBB. In this case, however, we can perhaps depart from the normal assumption that triploids have arisen directly from diploids. *M. balbisiana* is cultivated in the country and 'Kluai Teparod' (tetraploid ABBB) is known to be very female fertile in crosses with this species (Shepherd, 1960). The segregation of some triploids of apparently pure BBB phenotype is very possible from such a cross.

A Note on *Musa* Germplasm of the Philippines

The observations presented here are in response to the documents provided by the Director of INIBAP and to the circulated commentaries of the various investigators. I have treated matters concerning taxonomy as a separate review paper, which I hope will be of interest. On other themes I would first like to pose two questions.

1. Why has so little weight been given to the research performed at the University of the Philippine's Institute of Plant Breeding? Ramon Valmayor and his co-workers were fully aware of the earlier publications on Philippine cultivars and they have had the advantage of being able to study there more than 200 accessions in the uniform environment of Los Baños, rather than in scattered locations, where the accurate determination of synonymy is hardly possible. From these standpoints their 1981 list ought to be comprehensive and reliable, even though it fails to discriminate between the AA and AAA groups.

2. Are plantains so very important in the Philippines that unambiguous variation could be expected to have arisen? I feel that the answer to this question is in the negative. Dr. Swennen's comments on female fertility in plantains are of great interest, but his 'Muracho' seems to be more related to 'I aknai' than to plantains in the strictest sense. 'Laknau' (= 'Kune' in Papua New Guinea) is now widely known to be female fertile. Considering available resources, if there had to be a choice, I would prefer to see a survey of female fertility in known plantain variants than a search for new ones.

The mention of 'Muracho' raises the issue of nomenclature and the definition of 'plantain'. Paradoxically this is less of a problem in Peru where all cultivars

are plantanos or in Brazil where all are bananas. More confusing still is the use of 'plantain' in both the broad and the narrow senses to describe all clones whose fruit is starchy at ripeness or to refer only to the AAB subgroup. My suggestion is to restrict the use of the term *plantain* to the narrow sense definition of a subgroup (Horn, False Horn, Intermediate and French) in publications where misunderstanding is likely to occur. AAB forms with similar fruit would be described as 'plantain-like', including 'Laknai' and what I have referred to as Polynesian plantains such as 'Popoulu' and 'Maia Maoli'. Starchy bananas must be referred to as such.

I am not convinced that *M. Balbisiana* has a major role to play in the breeding of hybrid group cultivars. However, due to lack of interest and/or lack of resources, this species has not yet been studied intensively. As to female fertility, there is a big difference between diminished seed set (which may have diverse causes and be inconsistent within a clone) and parthenocarpy. Variability exists within the species in fruit numbers and in fruit size, but parthenocarpy would still surprise me if proven to exist. AAB and ABB cultivars presumably have many different B genomes since they must have come into being in different areas at different times.

What reason is there to suppose that the B genome of the Plantain subgroup is critically important to that group? It does not, for example, appear to contribute to the long fruits. The only diploid hybrid raised in Brazil from crossing the French plantain 'Terrina' is AA in phenotype and relatively long-fruited. Similarly, we have seen long-fruited AA hybrids from crosses of wild-type *M. acuminata* with the plantain-like AAB 'Sao Domingos' which, although quite different from 'Laknai', is also appreciably pollen fertile. In contrast, we have evaluated AB hybrids derived from 'Bluggoe' x wild-type *M. acuminata*. Despite their having 11 B chromosomes from 'Bluggoe', they are invariably non-parthenocarpic and disappointing in fruit size. It would seem to be more profitable to speculate on the origin of the A genome of the hybrid triploids as suggested by Tezenas du Montcel.

In relation to a description of 'Maduranga' in another work, I would like to make a contribution to the definition of 'Pacha Bontha Bathees' (PBB). Based on material in the Trinidad collection, subsequently lost to race 2 of Panama disease in Jamaica, PBB is closely related to 'Bluggoe' and forms part of what I regard as the Bluggoe subgroup. In addition to dwarfing, which seems to have occurred only in the Western Hemisphere, there are three principal mutations in the subgroup which appear in various combinations in India. The best known of these is the waxy-fruited variant. The second mutation is differentiated by the pronounced cylindrical apex of its fruits ('Monthan' or 'Bonthan' in India) in contrast to fruits with a tapered apex ('Nalla Bontha'). The third variant is the 'bathees' mutant where the female phase is prolonged by the addition of several clusters of smaller fruits. In fact, plants of 'Bontha bathees' that had reverted to 'Monthan' were seen by the author in the Trinidad collection. In reference to 'Maduranga', an average of 6.8 hands does not suggest 'PRR'.

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