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BOTANICAL CLASSIFICATION OF COFFEE

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Introduction

While the international coffee trade is concerned with only two coffee species — *Coffea arabica* and *C. canephora* — botanists regard as coffee trees all tropical plants of the *Rubiaceae* family, which produce seed resembling coffee beans. During botanical explorations of the tropical regions, from the sixteenth century onwards, wild coffees also attracted the attention of explorers and botanists. Their specimens are found in the herbaria and the names of the most famous explorers have been commemorated in both specific and generic epithets. Hundreds of species have been described, but the taxonomic classification of the genus *Coffea* has become very complex and rather confused.

Even the most authoritative classification system of Chevalier (1947) is now due for revision in view of the many new species discovered over the past 20 years on Madagascar (Leroy, 1961a, b, c, 1962, 1963, 1972a, b) and in East Africa (Bridson, 1982).

In addition the conventional methods of taxonomic classification, which are mainly based on morphological characteristics of specimens deposited in herbaria, are inadequate to give full justification to the tremendous variability encountered in the allogamous wild coffee populations.

In their efforts to develop a more exacting system of classification, coffee botanists and geneticists (Charrier, 1978; Berthaud, 1985) have followed the trend of modern taxonomy, which today makes use of a variety of scientific disciplines, to reflect the true genetic-historical relationship among plants and animals (Clausen, Keck and Hiesey, 1945; Dobshansky, 1970; Mayr, 1970; Harlan and de Wet, 1971).

This chapter presents a review of advances made in the taxonomy of coffee, starting with the standard classification based on herbaria specimens and living collections. This will then be followed by an analysis of data from studies of cytotaxonomy and cytogenetics, ecology and plant geography, as well as on biochemical and serological affinities, which have all contributed valuable knowledge needed for a better coffee classification.

Detailed botanical descriptions of cultivated coffee species have been presented earlier by various authors (Wellman, 1961; Haarer, 1962; Coste, 1968; Carvalho *et al.*, 1969) and therefore need not be repeated here.

Taxonomy

The first botanical description of a coffee tree, under the name *Jasminum arabicanum*, was made in 1713 by A. de Jussieu, who studied a single plant originating from the botanic garden of Amsterdam. However, Linnaeus (1737) classified it as a separate genus *Coffea* with the then only one known species *C. arabica*.

Many new species of *Coffea* have been discovered during exploration of the tropical forests of Africa since the second half of the nineteenth century. Several botanists have tried to describe these species, but this led often to confusion and numerous epithets have proved to be synonymous. Special mention should be made of the extensive taxonomic work of Chevalier (1947) on the *Coffea* species of Africa and Madagascar and of Lebrun (1941), who paid particular attention to the coffees of Central Africa, especially those found in Zaire.

Figure 2.1: Coffee Type Placentation

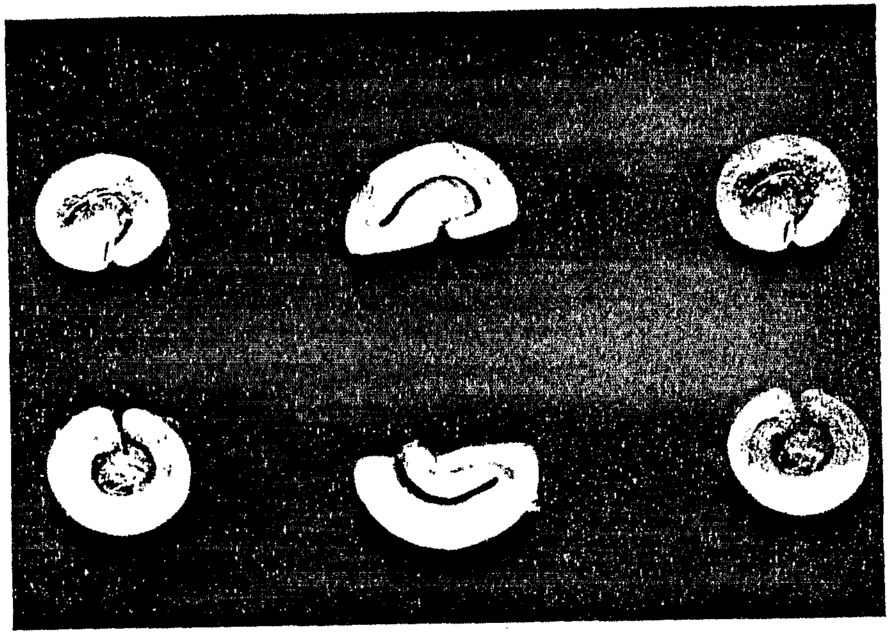


Table 2.1: Classification System for the Genera *Coffea* and *Psilanthus* According to Leroy (1980), with Indication of Geographical Distribution

Family:	*Rubiaceae,*	Subfamily:	*Cinchonoidea*
	Genus	SubGenus	Localisation
	Coffea L.	· *Coffea*	Africa, Madagascar
		· *Psilanthopsis* (Chev.)Leroy	Africa
		· *Baracoffea* (Leroy) Leroy	Africa, Madagascar
	Psilanthus (Hook.f.)	· *Paracoffea* (Miquel) Leroy	Africa, Asia New Guinea
		· *Psilanthus* (Hook. f.)	Africa

Table 2.2: The Two Criteria used by Leroy (1980) to Differentiate Genera and Subgenera

		Criterion 1	
		— Long corolla tube — Anthers not exserted — Short style	— Short corolla tube — Anthers exserted — Long style
		GENUS: *Psilanthus*	GENUS: *Coffea*
Criterion 2	· Axillary flowers · Monopodial development	*P.* Subgenus *Psilanthus*	*C.* Subgenus *Coffea*
	· Terminal flowers · Predominantly sympodial development	*P.* Subgenus *Paracoffea*	*C.* Subgenus *Baracoffea*

Of recent date are the detailed taxonomic studies of Leroy (1967, 1980) on the coffee species of Madagascar and of Bridson (1982) on the coffee species found in East Africa. Especially Leroy's (1980) efforts to indicate the relationship between species of the genus *Coffea* and those of *Psilanthus* and others are of particular importance to the understanding of the whole *Coffea* spectrum. His most important criteria for differentiating the genus *Coffea* from all other genera within the family *Rubiaceae* are the type of gynaecium and placenta (Figure 2.1) The classification system proposed by Leroy (1980) for the genera *Coffea* and *Psilanthus*, with indication of geographical distribution of the sub-genera, is presented in Table 2.1. The differentiation between genera and sub-genera is based on two main criteria (Table 2.2):

(1) flower shape, more in particular the length of the corolla tube (long or short) associated respectively with exerted anthers and style (Figure 2.6-2) or inserted anthers and short style (Figure 2.6-1).
(2) growth habit and type of inflorescence: monopodial with axillary flowers or sympodial with terminal flowers.

However, the second criterion is not unconditional, as both growth habits can occasionally be found on the same plant in some species.

On the other hand, Chevalier (1947) tried to group the species within the genus *Coffea* into the following four sections:

Argocoffea, Paracoffea, Mascarocoffea, Eucoffea.

According to Leroy's (1967) classification *Argocoffea* should be excluded fom the genus *Coffea*, because the seeds do not resemble coffee beans, and the section *Paracoffea* should be considered as a sub-genus of *Psilanthus* (Table 2.1). The section *Eucoffea*, now more correctly named *Coffea*, and *Mascarocoffea* include most of the presently known coffee species.

Coffea

This is divided into five subsections according to very diverse criteria: tree height (*Nanocoffea*), leaf thickness (*Pachycoffea*), fruit colour (*Erythrocoffea, Melanocoffea*) and geographical distribution (*Mozambicoffea*). The species grouped under each subsection are shown in Table 2.3.

Lebrun (1941) proposed the following series for *Coffea* species found in Central Africa, using the increasingly complex structure of the inflorescence as main criterion:

Abyssinicae, Robustae, Libericae.

The *Libericae* series contain a single species, because all the species with thick leaves and large fruits recognised by Chevalier were placed in synonymy with *C. liberica* by Lebrun. Consequently, the subsection *Pachycoffea* of Chevalier becomes equivalent to the series *Libericae* of Lebrun and to *C. liberica* in a broad sense. Chevalier saw during his taxonomic studies only a few herbarium specimens of coffee species from East Africa, but nevertheless observed the originality of this material. Bridson (1982) carried out detailed studies on coffee species for the *Flora of Tropical East Africa* (not yet published). A list of coffee species and taxa found in this part of Africa, many of which are still incompletely known, is given in Table 2.4. Many of these coffee species are well adapted to drier climates by their xeromorphic characteristics and the short interval between flowering and mature seed (only three months versus 8-12 months for most other coffee species).

Mascarocoffea

The coffee species belonging to this section all have one characteristic in common: the absence of caffeine, which was first reported by Bertrand (1902). The tremendous variety in forms has hampered taxonomic classification. A first regrouping of species in series was made by Chevalier (1938), but in view of the more than 50 different forms (Portères, 1962; Leroy, 1961a, b, c, 1962, 1965, 1982) found within material collected during the early 1960s Leroy proposed a revision of the series within the *Mascarocoffea* section (Table 2.5). This classification takes into account leaf, fruit and seed characteristics. Charrier (1978) gives in his synthesis on *Mascarocoffea* a concise botanical description of all known species with details of their geographical distribution on Madagascar.

Of considerable interest are also the efforts of Lobreau-Callen and Leroy (1980) and Chinnappa and Warner (1981) to establish a palyno-

Table 2.3: The Grouping of Species in the Subsection *Eucoffea* According to Chevalier (1947)

Subsections	Species
Erythrocoffea	*C. canephora* *C. arabica* *C. congensis*
Pachycoffea	*C. abeokutae* *C. liberica* *C. klainii* *C. oyemensis* *C. dewevrei*
Melanocoffea	*C. stenophylla* *C. carissoi* *C. mayombensis*
Nanocoffea	*C. humilis* *C. brevipes* *C. togoensis*
Mozambicoffea	*C. schumanniana* *C. eugenioïdes* *C. kivuensis* *C. mufindiensis* *C. zanguebariae* *C. racemosa* *C. ligustroides* *C. salvatrix*

Table 2.4: List of Taxa of *Coffea* from East Africa Adapted from Bridson (1982)

C. fadenii
C. mongensis
C. kivuensis
C. salvatrix
C. pseudozanguebariae
C. sp. A
C. sp. B
C. sp. C
C. sp. D
C. sp. E
C. sp. F
C. sp. G
C. sp. H
C. sp. I
C. mufindiensis
— subsp. *mufindiensis*
— subsp. *lundaziensis*
— subsp. *autralis*
C. pawekania
C. ligustroïdes
C. zanguebariae
C. racemosa
C. sp. J
C. sp. K
C. paolia

Table 2.5: List of the 'Series' proposed by Chevalier (1938) and Revised by Leroy for the *Mascarocoffea* of Madagascar

Series:		
— *Verae*	Chev.	
— *Multiflorae*	Chev.	
— *Sclerophyllae*	Chev.	
— *Brachysiphon*	Dubard	
— *Terminales*	Chev.	
— *Garcinioïdes*	Chev.	
— *Mauritianae*	Chev.	*Mauritianae* Chev.
— *Macrocarpae*	Chev.	*Humblotianae* Ler.
— Unclassed		

logical basis for coffee taxonomy. It enables differentiation at the generic level, as the 3-porate pollen of *Coffea* species is easily distinguished from the 4-5 porate pollen of *Psilanthus* and *Paracoffea* species. Unfortunately, the eight morphologically different types of pollen described by Chinnappa and Warner (1981) bear little relation to the subsections and series in the taxonomic classification of the genus *Coffea.*

The wealth of forms encountered in wild coffees is the result of the interaction of the genetic variability of coffee populations with an endless range of ecological 'microniches' (Forster, 1980) of natural habitats. Botanists have often failed to take this variation into account by restricting themselves mostly to morphological characters, when they tried to establish clear-cut distinctions between species in which genetic differentiation is still occurring.

Souces of Botanical Information

Information on coffee species in relation to habitats, taxonomic characteristics, genetic diversity and geographical distribution can be found in herbaria, travel reports of botanical explorers and in the living collections of research stations.

Major Herbaria

Because of the historical ties with Africa and South East Asia most European botanists of earlier times sent their collections to herbaria in their home countries, with the result that these herbaria are characterised by a high degree of geographical specialisation. This applies also to the herbarium specimens of coffee, which are therefore important sources of information for botanists when preparing new missions to collect and preserve coffee genetic resources in centres of genetic diversity in Africa. Below follows a brief description of the herbaria most relevant for coffee:

(1) The Royal Botanic Garden at Kew and the Natural History Department of the British Museum in London, UK: comprehensive collections from the Sudan, Uganda, Kenya, Tanzania and other eastern and southern African countries, as well as from English speaking West Africa and Angola.

(2) Jardin Botanique National de Belgique at Meise, Belgium: with emphasis on Zaire.

(3) Museum National d'Histoire Naturelle at Paris, France: with comprehensive collections from Guinea, Ivory Coast, Cameroon, Gabon, Congo, the Central African Republic and the Malagasy Republic.

(4) Botanische Garten und Botanische Museum at Berlin-Dahlen, Germany: with collections from Togo, Cameroon and Tanzania, which were however almost completely destroyed in 1943.

(5) Herbarium Vadense of the Department of Plant Taxonomy and Geography of the Agricultural University of Wageningen and the Rijksherbarium of the University of Leiden, The Netherlands: with coffee specimens from respectively Africa (especially Cameroon) and Indonesia.

(6) Erbario Tropicale di Firenze, Florence, Italy: collections from Ethiopia and Somalia.

(7) Botanical Institute of the University of Coimbra and Centro de Botanica da Junta de Investigaçoes Cientificas do Ultramar at Lisbon, Portugal: with collections from Angola and Mozambique.

These European herbaria may already give a very good imprèssion of the overall distribution of the wild coffees. Nevertheless, the importance of national herbaria in Africa should not be underestimated, as they often represent part of the duplicate herbarium specimens sent to Europe and some have also extended their collections through their own explorations.

A comprehensive list covering all the coffee specimens present in the herbaria of Europe and Africa is lacking. It would be very difficult to realise, because determinations made are sometimes inaccurate or only approximate descriptions. Many of the collected plants have still to be determined taxonomically and to be classified.

Natural Habitats of the Wild Coffees

Wild coffee trees are components of the understorey of tropical forests in Africa. The observations made by collectors include precise descriptions of habitats, which are quite distinct for *C. arabica* and other coffee species.

C. arabica. All botanists, who have explored the forests on the southwestern highlands of Ethiopia, agree in their observation that this is the centre of diversity of *C. arabica*, but that it is very difficult to find truly wild populations (Sylvain, 1955; Von Strenge, 1956; Meyer, 1965; Friis, 1979).

This species is indeed very common to the understorey of the forest, but most of the trees are regularly harvested by the local people, who usually carry out some form of maintenance by clearing the bush to facilitate picking of the ripe cherries. Guillaumet and Hallé (1978) distinguished the following stages from practically wild to truly cultivated coffee plots: (a) natural populations maintained *in situ*; (b) populations improved by introduction of young coffee trees from elsewhere; (c) farmers' plots established with plant material derived from wild coffee trees.

On the other hand, Thomas (1942) found in secondary forest on the Boma plateau in south-eastern Sudan truly wild populations of *C. arabica*, which apparently grew there without human interference.

Semi-wild populations of *C. arabica* can also be found at an altitude of about 1500 m in the upland forest on Mt Marsabit in north Kenya (Berthaud, Guillaumet, Le Pierrès and Lourd, 1980). It is not clear, whether these trees are truly wild or in earlier times brought from Ethiopia by man.

The Other Coffee Species. Apart from some subspontaneous populations of *C. liberica* and *C. canephora* found in Ivory Coast and Central Africa, most other wild coffee species appear to grow in their natural habitat, which consists of the understorey of tropical forests. However, these forests are an extremely complex and organised environment. All the collectors have noticed a really specific adaptation of coffee trees to elevation, altitude, rainfall and soil types.

In East Africa rainfall is largely controlled by altitude and mountains stand out as wet areas covered in dense forest (Lind and Morrison, 1974). Typical examples are found in Kenya: Mt Marsabit with *C. arabica* and the Taita Hills with *C. fadenii*. In contrast, where variations in altitude are much less pronounced as in West Africa, the well-drained hill tops are the driest zones. For example, in the Ira forest of Ivory Coast *C. stenophylla* grows on the top of the hill, while *C. canephora* and *C. liberica* occupy the lower humid zones (Figure 2.2). This location of *C. stenophylla* populations is common in the western part of the Ivory Coast and is an indication of its specific adaptation to dry conditions. In the eastern part of that country *C. stenophylla* is found in the dry lowlands with a semi-deciduous type of forest.

C. humilis represents a good example of the importance of the biotope: whatever the altitude, this species grows in the small talwegs and at the border of swamps of south-western Ivory Coast. This species is able to grow in very wet environments, which would explain its limited area of distribution. Thomas (1944) reported that in Uganda *C. eugenioides* is always found in the drier zones of the forest and *C. canephora* in more humid environments.

In the Central African Republic Berthaud and Guillaumet (1978)

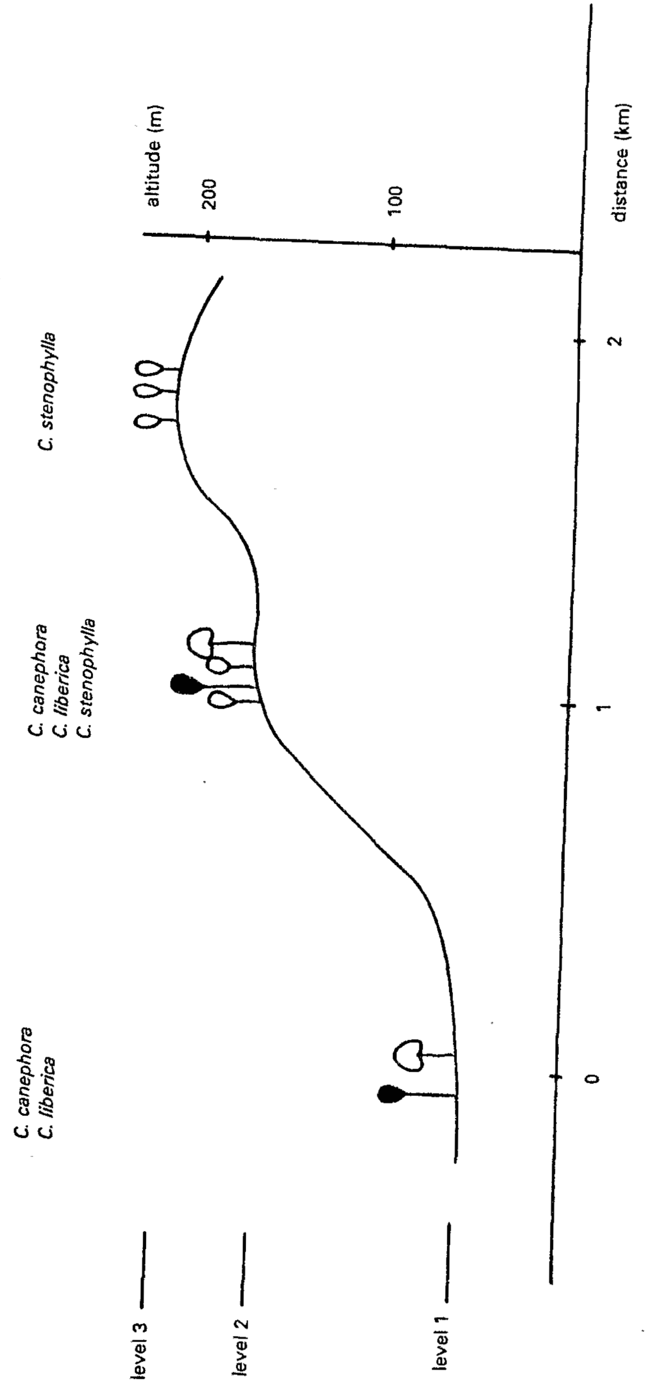


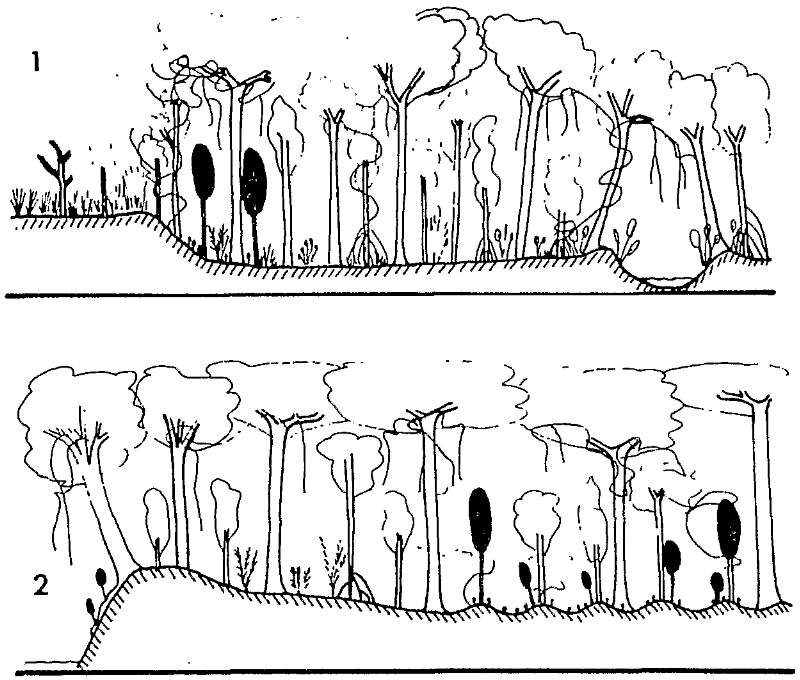
Figure 2.2: Spatial Distribution of the Coffee Species According to Topography in the Ira Forest (Ivory Coast)

observed also the presence of *C. dewevrei* in the periphery of gallery forests bordering savannah land, where the soil is well-drained (Figure 2.3-1). In the same country *C. congensis* was found on the eroded banks of the Oubangui river and on sandy islands, but always in seasonally flooded areas. When the river is high, the coffee roots hold the sandy soil in place, with the result that each coffee tree stands on a little hillock (Figure 2.3-2).

On Madagascar, within the same geographical area where *C. resinosa* and *C. richardii* are found together, the distribution of the two species is closely associated with pedological characteristics: spodosols for *C. resinosa* and oxysols for *C. richardii.*

The habitats of the various coffee species correspond closely with specific biotopes and these should, therefore, be very well known in order to be able to discover wild coffee populations. Such ecological data are also essential for selecting appropriate growing conditions for living collections and testing of the agronomic qualities for cultivation.

Figure 2.3: Cross Section of Wild Coffee Habitats. 1. *C. dewevrei* (in dark) at the periphery of a gallery forest (Lihou — Central African Republic). 2. *C. congensis* (in dark) on sandy banks and small hillocks (Louma island — Central African Republic). (From Berthaud and Guillaumet, 1978.)



Collecting Missions for Wild Coffee Species

As already mentioned, exploration for wild coffee species started together with that of other tropical plants in the sixteenth century and was particularly intense in Africa towards the end of the last century and during the first part of the twentieth century. Evidence for that era is mostly found in herbaria and very little in the existing living collections.

Of course, all coffee research centres maintain collections of the cultivated coffee species. These working collections are used for the improve-

Table 2.6: Coffee Collecting Missions Since 1960

Years	Countries explored	Organisations	Collectors' names	Coffee species	Germplasm maintenance countries
1964	Ethiopia	FAO	Meyer Monaco Narasimhaswamy Fernie Greathead	*C. arabica*	Ethiopia India Tanzania Costa Rica
1966	Ethiopia	ORSTOM	Guillaumet Hallé	*C. arabica*	Ethiopia Madagascar Ivory Coast Cameroon
1960 to 1974	Madagascar Mauritius Reunion Island Comoro Islands	Museum IFCC ORSTOM	Leroy Portères Vianney-Liand Guillaumet Charrier	*Mascarocoffea* (up to 50 taxa)	Madagascar
1975	Central Africa Republic	ORSTOM IFCC	Guillaumet Berthaud	*C. congensis* *C. dewevrei* *C. canephora* Caféier de la Nana	Ivory Coast Central African Republic
1975 to 1980	Ivory Coast	ORSTOM	Berthaud	*C. liberica* *C. stenophylla* *C. canephora* *C. humilis* *Paracoffea* sp. *Psilanthus* sp.	*Ivory Coast*
1977	Kenya	ORSTOM IFCC	Berthaud Guillaumet Lourd	*C. arabica* *C. eugenioïdes* *C.zanguebariae* *C. fadenii*	Kenya Ivory coast
1982	Tanzania	ORSTOM IFCC	Berthaud Anthony Lourd	*C. zanguebariae* *C. mufindiensis* C. sp.	Tanzania Ivory Coast
1983	Cameroon	ORSTOM IFCC	Anthony Couturon de Namur	*C. canephora* *C. liberica* *C. congensis* *C. brevipes* *C.* sp. *Psilanthus* sp.	Cameroon Ivory Coast

ment of *C. arabica* and *C. canephora.* Such collections have been extended regularly by introductions of more or less selected plant material from other coffee stations, botanic gardens or local plantations. The other coffee species are usually scarcely represented.

Awareness of the lack of variability in the existing coffee collections made the FAO and French organisations (ORSTOM, IRCC, the Museum at Paris) intensify their efforts to collect coffee germplasm during the last twenty years. The most important collecting missions are listed in Table 2.6, with indication of the countries covered, names of the collectors, the species collected and the countries where the material is maintained (Meyer *et al.*, 1968; Charrier, 1980; Berthaud, Guillaumet, Le Pierrès and Lourd, 1977; Leroy, 1961a, b, c, 1962, 1963, 1982). Emphasis in the collection of coffee germplasm was particularly on *C. arabica* because of its economic importance, but a number of non-cultivated species have also been collected, such as those of the section *Mascarocoffea* (caffeine free), the subsection *Pachycoffea, C. congensis* (progenitor of the Congusta hybrids), *C. eugenioides* (presumed progenitor of the allotetraploid *C. arabica*) and of the related genus *Psilanthus.*

Living Collections

A comprehensive botanical study should also include the World living collections of coffee. The FAO prepared an inventory of the existing coffee collections in 1960 (Krug, 1965) and this was updated in 1978-79 (unpublished). However, these reports do not fully reflect the actual importance and extent of the genetic diversity of the living collections. The location of living collections is depicted in Figure 2.4.

Important collections of *C. arabica* with material of the Ethiopian centre of genetic diversity are present at Jimma (Ethiopia), Turrialba (Costa Rica), Campinas (Brazil), Chinchina (Colombia), Lyamungu (Tanzania), Ruiru (Kenya), Foumbot (Cameroon), Man (Ivory Coast) and Ilaka-Est (Madagascar). There is a unique collection of species of the section *Mascarocoffea* at Kianjavato (Madagascar).

The main African coffee species are kept in the living collections at Divo and Man in Ivory Coast: more than 10 species of the section *Coffea* are represented by hundreds of thousands of genotypes collected from natural populations in different countries since 1965 (Table 2.6).

At the same time the working collections of *C. arabica* and *C. canephora* maintained in India, Cameroon, Togo, Angola and other countries also contain very valuable material.

In tropical Africa one can find, at least for the time being, wild coffee trees in undisturbed forests and subspontaneous coffee in traditional agricultural areas. However, it has become a matter of urgency to continue with the collection of coffee germplasm, where the natural habitats are being threatened by human activities.

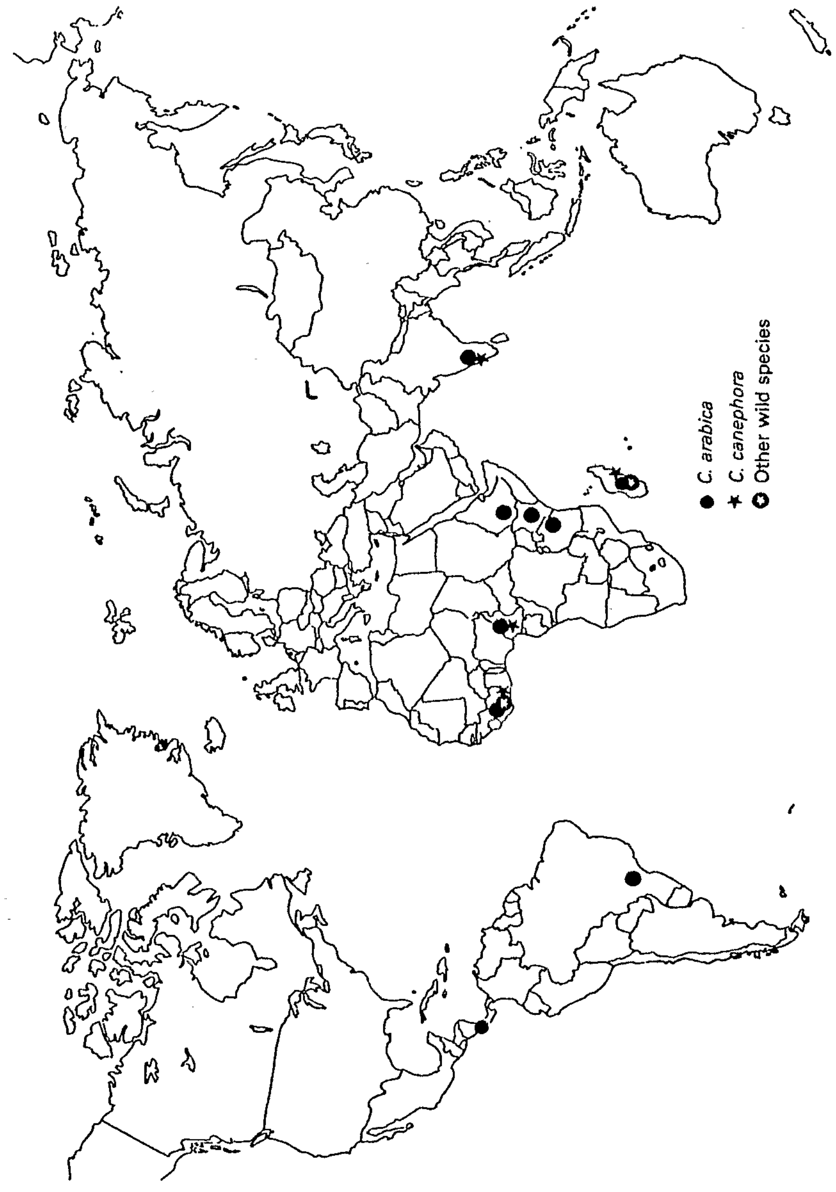


Figure 2.4: Existing Living Collections of Coffee Species in the World

Figure 2.5 presents a map of Africa, indicating the areas of origin or high genetic diversity for coffee species of the sections *Coffea* and *Mascarocoffea*. This map is based on accumulated information from herbaria, collecting missions and living collections.

Cytotaxonomy and Reproductive Systems

Chromosome Number

Results of studies on chromosome numbers in coffee carried out since the 1930s have been reviewed by Sybenga (1960). The basic genome of the genus, $x = 11$ chromosomes, is typical for most of the genera of the family *Rubiaceae*. Chromosome counts were made for most species of the genus *Coffea* and for some representatives of the genus *Psilanthus*.

In the section *Coffea* all species are diploid with $2n = 22$ chromosomes, except for the tetraploid *C. arabica* which has $2n = 4x = 44$ chromosomes.

In the section *Mascarocoffea* the chromosome number of more than 20 species has been determined (Portères, 1962; Leroy and Plu, 1966; Friedman, 1970; Louarn, 1972). Species belonging to this section are all diploid ($2n = 22$) and the very large variability encountered in this section cannot therefore be attributed to variation in chromosome number.

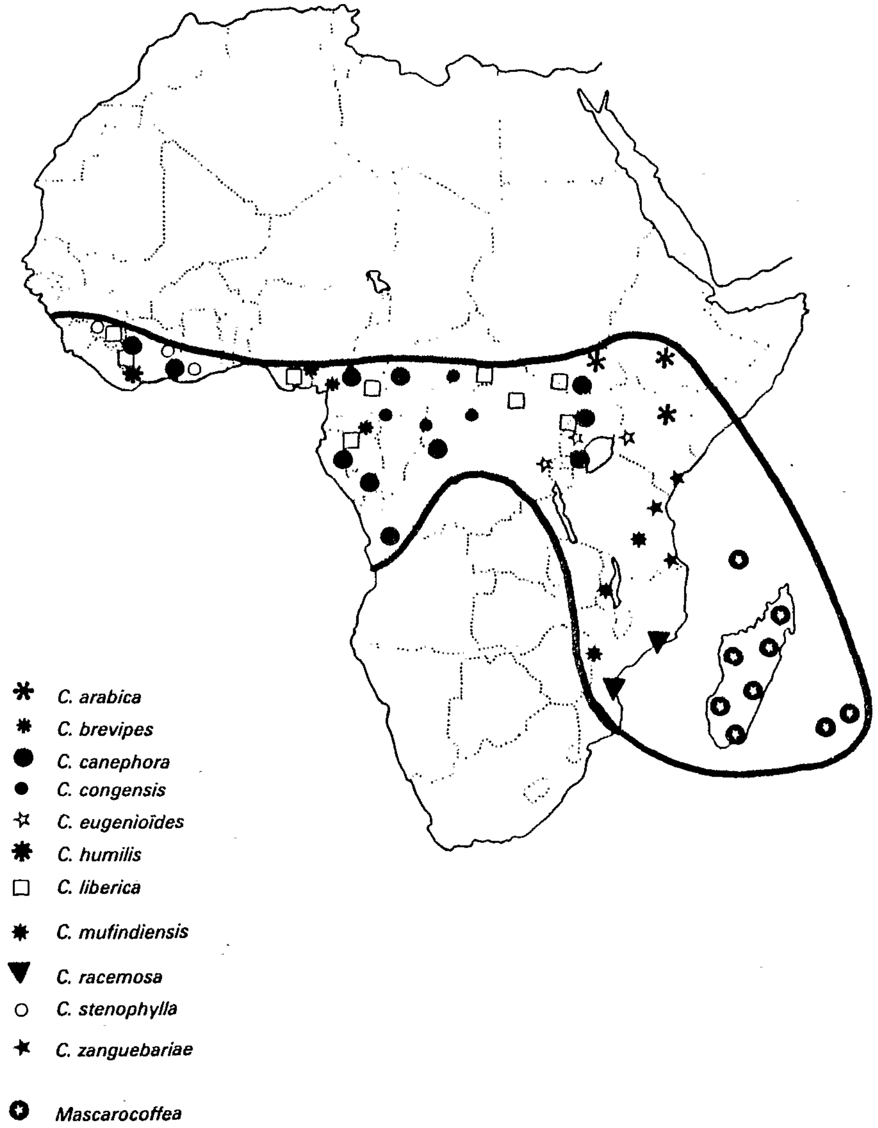
In the genus *Psilanthus* the chromosome number $2n = 22$ has been confirmed for *P. humbertii* (Leroy and Plu, 1966), *P. horsfieldiana* (Bouharmont, 1959), *P. bengalensis* (Fagerlind, 1937) and *P. mannii* (Couturon, personal communication).

Deviations from the normal chromosome number do occur in exceptional cases. For example, in *C. arabica* a whole series of polyploids have been found (Sybenga, 1960): triploids ($3n = 33$), pentaploids ($5n = 55$), hexaploids ($6n = 66$) and octoploids ($8n = 88$). Haploids, or more correctly called di-haploids with $n = 2x = 22$ chromosomes, occur in low frequencies in seedling offspring as weak plants with narrow leaves and have been called *monosperma* (Mendes and Bacchi, 1940).

Diploid *C. canephora* with sectorial tetraploid chimaeras have been found and induction of artificial autotetraploidy by colchicine treatment of germinating seed (Mendes, 1939) or shoot apices (Berthou, 1975; Noirot, 1978) is possible. Methods of recovering the naturally occurring haploid plants in *C. canephora* have been developed recently (Couturon and Berthaud, 1982). Doubling with colchicine results in homozygous plants of *C. canephora*, which are of great interest to coffee breeding (see Chapter 3).

The morphology of coffee chromosomes was studied by Mendes (1938) and Bouharmont (1959, 1963). The latter author described some 10 species and prepared an average idiogram for the 11 chromosomes of the basic genome for the genus *Coffea*. Coffee chromosomes are relatively

Figure 2.5: Natural Distribution of Coffee Species in Africa and Madagascar



small (1 — 3μm), but modern methods of staining chromosomes (banding) open up possibilities of studying the chromosome morphology in more detail.

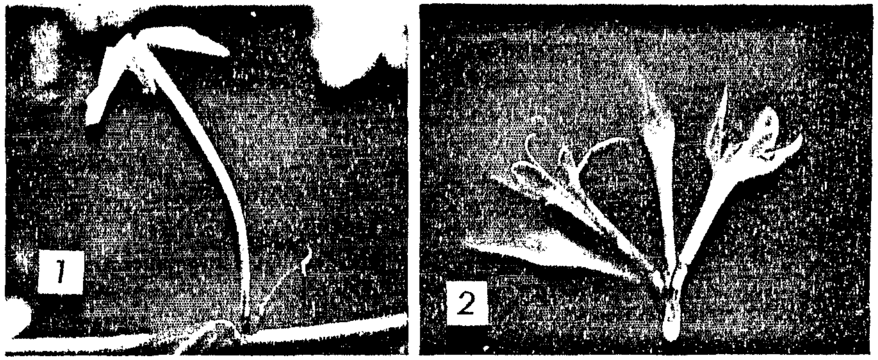
Reproductive Systems

Psilanthus. In this genus flowers have a short style and long corolla tube (Figure 2.6-1). System of incompatibility appears to be absent and most species, e.g. *P. bengalensis*, are autogamous. However, occasional cross pollination and consequently genetic exchange may occur, as heterozygous plants have been found after analysis by electrophoresis.

Coffea arabica. Flowers of this species are typical of the genus *Coffea*: short corolla tube, long style and exerted stamens (Figure 2.6-2). Such morphology would permit natural cross pollination, but nevertheless *C. arabica* is largely autogamous. Fruit set after self pollination is 60 per cent or higher (Carvalho *et al.*, 1969). In Ivory Coast, Le Pierrès (personal communication) effected self pollination on 32 trees of F_1 progenies of crosses between various accessions of *C. arabica* from Ethiopia. Of the 8,400 flowers 5,400 set fruit after self pollination. This means a success rate of 65 fruits to 100 flowers. However, this percentage varied from 3 to 91 per cent between trees, which could indicate variation in the degree of self fertility in wild populations of *C. arabica*. Meyer (1965) reported 40-60 per cent cross pollination in wild populations of *C. arabica* in Ethiopia.

Most studies on the degree of natural cross pollination were carried out on cultivars of *C. arabica*, which underwent many cycles of selection. By using the recessive marker genes *Cera* (yellow endosperm) and *Purpurascens* (purple leaves) Carvalho and Krug (1949) in Brazil and Van der Vossen (1974) in Kenya found percentages of natural out-pollination ranging from 7 to 15 per cent.

Figure 2.6: 1. Flowers of *Psilanthus*, on the Right: Flower with Removed Corolla; 2. Flowers of *Coffea*



Diploid Species of the Genus Coffea. Most diploid coffee species have proved to be highly self incompatible including 24 tested species of the section *Mascarocoffea*. Devreux, Vallayes, Pochet and Gilles (1959) describe how, after self pollination, pollen tube growth on the stigma of *C. canephora* becomes distorted and further penetration into the style is blocked. Berthaud (1980) produced further evidence for a gametophytic system of incompatibility in *C. canephora*, which is controlled by one gene with multiple alleles. A similar mechanism appears to operate also in Congusta coffee (a hybrid between *C. congensis* and *C. canephora*). On the other hand, observations on *C. liberica* indicate that the incompatibility reaction can be delayed until the day of anthesis. Penetration of the pollen tubes in the stigma and style could take place with 'bud pollination' (Hamon, personal communication).

One notable exception appears to be an accession in the living coffee collections in Ivory Coast of unknown origin but resembling *C. brevipes* and self-compatible (Le Pierrès and Louarn, personnal communication). We observed that some pollen tubes grow through the style while others were blocked at the papillary zone of the stigma, as in incompatible combinations. The offspring of such trees was very homogeneous. Could this mean mutation of an S allele making it inoperative?

Because of the high degree of self-incompatability in most diploid species, a high level of heterozygosity will be maintained in populations and this has great consequences to breeding (see Chapter 3).

Wild Populations of Coffea

The variability existing in natural coffee populations has been studied to a limited extent so far. Portères (1937) was one of the first to describe the variability of populations of *C. canephora*, *C. liberica* and *C. stenophylla* and their offspring in Ivory Coast. Considerable work was also carried out on Java on numerous progenies of introduced coffee species (Cramer, 1957).

Botanists and geneticists have in their recent efforts to explore and preserve coffee genetic resources applied various methods to describe the variability present in wild coffee populations, including: (a) morphological observations and numerical taxonomy; (b) analysis of electrophoretic variants; (c) studies of the frequency distribution of incompatibility alleles within and between populations; and (d) genetic analyses with progenies of controlled crosses.

A few examples of natural coffee populations may serve as an illustration.

Coffea arabica

The great variability in natural populations of *C. arabica* has been apparent to most botanists and geneticists, who visited and explored the south-western highlands of Ethiopia.

An electrophoretic analysis of six enzyme systems produced similar homogeneous patterns, both for accessions from Ethiopia and from Mt Marsabit in Kenya (Berthou and Trouslot, 1977, and unpublished). This made it possible to describe the electrophoretic type for *C. arabica*. It is of interest to note here, that this analysis generally pointed to an expression of two alleles at each locus, which would support earlier conclusions from classical genetic analyses (Carvalho *et al.*, 1969) that the allotetraploid *C. arabica* is a functional diploid for most gene expressions.

This uniformity of the species is lost if the morphological characteristics of germplasm collections (origin differences) or their progenies (family differences) are examined. Actually, hierarchical variance analysis carried out by Reynier, Pernes and Chaume (1978) and Louarn (1978) showed that differences between origins and between families are both significant, but with the interorigin variance component being several times higher.

The caffeine content of *C. arabica* germplasm from Ethiopia varies from 0.8 to 1.9 per cent (of dry matter), a variation not correlated with geographical distribution.

It is difficult to differentiate 'varieties' within this (semi-)wild material because of the considerable variation existing between trees of the same sub-population and such trees produce also heterogeneous progenies. The term variety (or cultivar) should therefore be reserved for the cultivated forms of this species, which are indeed homogeneous due to several generations of line selection.

C. canephora: the 'Nana' Population

This population is located in a gallery forest of the savanna zone in the Central African Republic and it represents the northern limits for the distribution of *C. canephora*. This material is well adapted to the climatic and pedological conditions of that area and it has been cultivated locally since 1923. The original population was rediscovered in 1975 (Berthaud and Guillaumet, 1978) and about 100 plants raised from seed and cuttings were added to the coffee collection in Ivory Coast.

Observations on morphological characteristics and floral biology indicate that there is considerable variation, but no sub-populations could be detected. Some characters like colouration of mature fruits appear to be fixed, while others are heterozygous. This was also confirmed by electrophoretic analysis. An analysis of incompatibility points to a considerable number of S alleles being present in that population.

Taxonomically, there is now sufficient evidence to consider the Nana population as part of the species *C. canephora*. The diversity found within this material appears similar to that encountered in other populations of *C. canephora*.

C. stenophylla

Wild populations of this species exist in west and east Ivory Coast. Phenotypically these populations are easily distinguishable as is shown in Table 2.7. Electrophoretic analysis indicates that these populations are very homogeneous but the alleles of the western populations differ from those fixed in the eastern ones. In a population of 1000 trees of western origin, the total number of S alleles was less than 10, which would suggest that the population originates from five parent trees at the most. Notwithstanding the expected relatively low genetic diversity, caffeine content determinations gave a range from 0.9 to 1.9 per cent (on dry matter), a variation similar to *C. arabica*.

The geographical isolation apparently produced considerable genetic diversity between populations, as interpopulation crosses gave distinct hybrid vigour.

C. zanguebariae

When examining herbarium specimens one realises that the specific name applies to two taxa, one without and one with fruit stalks. These forms are indicated here as A and B, which is synonymous with the taxa *Coffea* sp. *A* and *C. pseudozanguebariae* described by Bridson (1982). Various populations, collected in Kenya by Berthaud *et al.* (1980), are now under observation in Ivory Coast. The main characters of these two taxa are compared in Table 2.8. Analysis by electrophoresis has also indicated differences between the two taxa. Three of the studied populations were found to belong to form B, while one included both forms as well as intermediary types. Plants of the A form have all flowers open on the same day, while trees of form B flower over three consecutive days (Hamon *et al.*, 1984)

Hybridisation between the two forms is possible, although the chances of natural cross pollination between trees of the B form only should be higher.

Table 2.7: Morphological Characteristics of the Western and Eastern Forms of *C. stenophylla* in Ivory Coast

Observed character	Eastern form	Western form
Secondary branching pattern	very numerous branches	numerous branches
Leaves	very small	small
Flowers per fascicle	1	2
Flower shape	globulous	oblong
Fruit colour	black	black

Table 2.8: Morphological Characteristics of the A and B Forms of *C. zanguebariae*. (After Hamon and Anthony, to be published.)

	A form	B form
Leaf-thickness	thick	thin
Stipule length	long	short
Domatia	small	big
Day range between shower and first flowering	6	6
Number of flowering days	1	3
Corolla lobes number	5	6-7
Fruit stalk length	very short	long
Fruit colour before ripening	green	brown

However, Anthony (personal communication) and Louarn (1982) carried out crosses between trees of the A and B forms as well as between the A form and several other species. Crosses between A and B forms gave a considerably lower fruit set than crosses between the A form and for instance *C. eugenioides* and *C. racemosa*. It appears that a genetic barrier has evolved between the two forms but not due to geographic separation.

Such a genetic barrier had not evolved, however, between the earlier mentioned subpopulations of *C. stenophylla*, regardless of the considerable morphological differences.

C. liberica

This species also shows distinctly different forms: *C. liberica* var. *liberica* from West Africa (Guinea, Liberia, Ivory Coast) and *C. liberica* var. *dewevrei* from Central Africa (usually called Excelsa coffee). Forms of *C. liberica* found in Cameroon appear to be intermediate between these two extremes, but this still requires verification.

Mascarocoffea

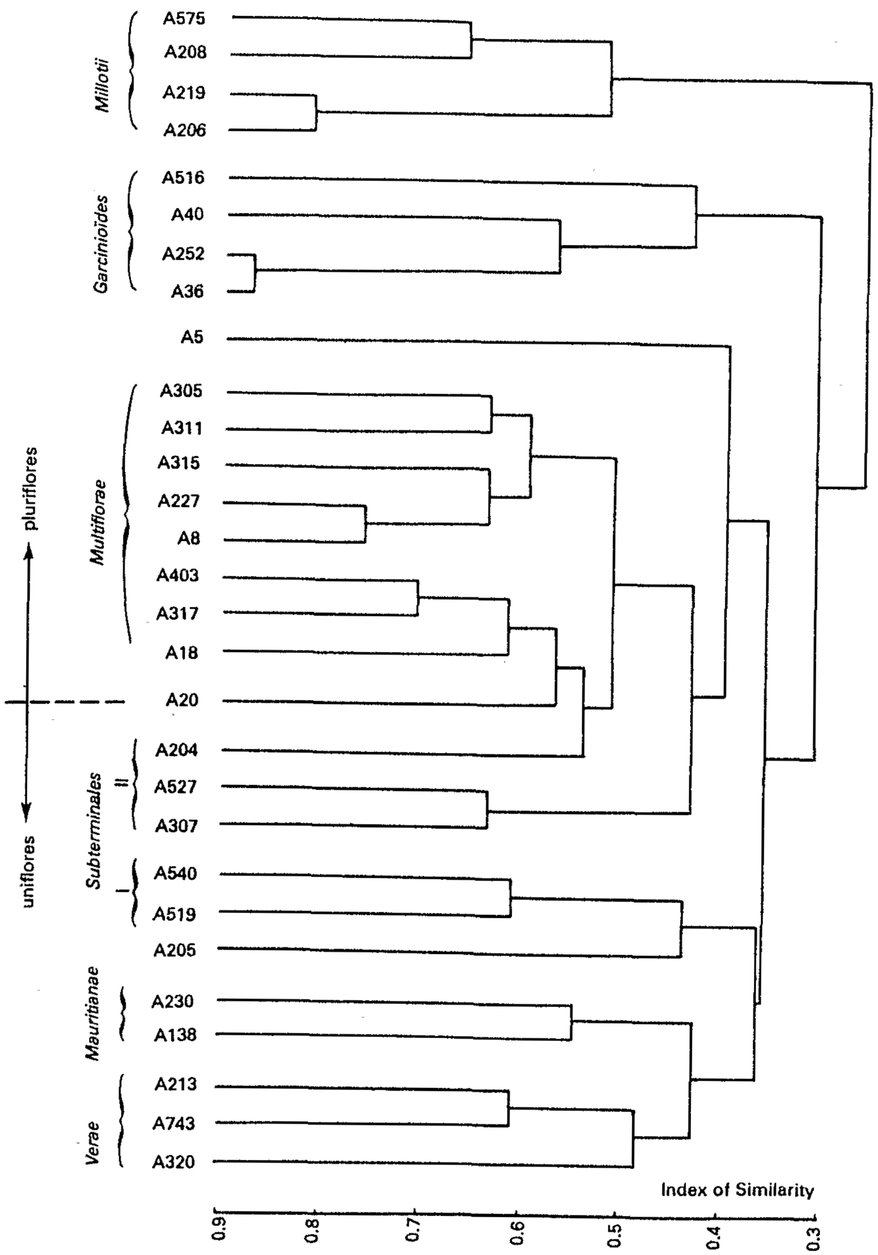
A large number of different species (or taxa) have been distinguished already (Charrier, 1978). However, the relatively high success of interspecific hybridisation within this section indicates that only weak genetic barriers have evolved. Figure 2.7 presents a hierarchical classification, mainly based on morphological characteristics.

Multispecific Populations

The existence of multispecific wild coffee populations is supported by observations made during various collecting missions carried out in the past 20 years.

Apart from the coexistence of the A and B forms of *C. zanguebariae* in one population in Kenya, the following associations have been encountered in Ivory Coast and in the Central African Republic:

Figure 2.7: Differentiation of the Taxa of *Mascarocoffea* by a Hierarchical Classification



— *C. liberica* + *C. canephora* (Gbapleu, Ivory Coast)
— *C. liberica* + *C. humilis* (Tai, Ivory Coast)
— *C. liberica* + *C. stenophylla* + *C. canephora* (Ira, Ivory Coast)
— *C. liberica* + *C. congensis* + *C. canephora* (Bangui, Central African Rep.)

Multispecific populations have also been found on Madagascar with species of the section *Mascarocoffea* (Charrier, 1978), while in Uganda associations of *C. canephora* with *C. liberica* or *C. eugenioides* have been reported by Thomas (1944).

These observations made on wild coffee populations strongly suggest that:

(1) hybridisation between geographically adjoining species in wild populations occurs only sporadically. On Madagascar hybrids between two species were found on two occasions, while in Ivory Coast occasional interspecific hybrids were noticed in the seed progeny of wild coffee trees;
(2) interspecific hybrids represent a transitory state, which may explain why they are rarely encountered in natural conditions.

Various factors appear to restrict chances of gene exchange between species in multispecific populations:

(1) species coexist more side by side within a limited area rather than in a real mixture: their separation can be due to microclimatic (different sides of a hill), pedologic (different soils) or topographic differences;
(2) flowering patterns differ between species: *C. canephora* usually flowers early in the year, while *C. liberica* and *C. stenophylla* tend to flower later: the time interval between a flowering inducing rainshower and anthesis is also often one day longer for *C. canephora* than for *C. liberica.*

Clearly, studies of wild coffee populations have contributed considerably to a better understanding of the relation between species of multispecific associations. Genetic exchange between coffee species through interspecific hybridisation should be taken into account when formulating theories on the evolution of coffee species.

Evolution of the Coffee Gene Pool

Most studies on the genetic relationships of species in the genus *Coffea* before 1960 were almost entirely restricted to the subsection *Erythro-*

Table 2.9: Review of the Cytogenetic Behaviour of Interspecific Crosses Between Diploid *Coffea* Species

Diploid F$_1$ hybrids	Chromosome associations		PMC with 11 bivalents %	Pollen fertility	References
	Univalents	Bivalents			
C. canephora × *C. congensis*	0.04-0.74	10.63-10.98		high	Leliveld (1940)
	0.20-0.52	10.74-10.90	74-90	89-93	Charrier (1978)
C. liberica × *C. dewevrei*	Normal meiose (Rhoades)			high	Carvalho and Monaco(1968)
C. canephora × *C. dewevrei*	1.44	10.28		middle	Leliveld (1940)
C. canephora × *C. liberica*	0.30-1.40	9.93-10.66		39	Chinnappa (1970)
C. canephora × *C. neo-arnoldiana*	1.16-1.20	10.40-10.42	50-58	64	Louarn (unpublished)
C. canephora × *C. eugenioides*	1.30-2.22	9.89-10.35	23-44	43	Louarn (1976)
Liberio-excelsoides × *C. eugenioides*	about 2 I				Vishveshwara (1975)
C. canephora × *C. kapakata*	1.28-1.64	10.18-10.36	42-48	35	Louarn (unpublished)
	1.50	10.25		middle	Leliveld (1940)
C. canephora × *C. lancifolia*	3.20	9.40	8	8	
C. canephora × *C. resinosa*	4.40-6.40	7.80-8.80	0-2	4-7	Charrier (1978)
C. canephora × *C.* sp A311	5.04	8.48	4	6	

coffea. More recently, however, the crossability and chromosomal homology among other coffee species have received much attention, particularly in Brazil (Carvalho and Monaco, 1968), India (Vishveshwara, 1975), Madagascar (Charrier, 1978) and in Ivory Coast (Capot, 1972; Louarn, 1982). Coffee taxonomists have also started to establish the biochemical and serological affinities of coffee taxa through research on enzyme polymorphism, cytoplasmic DNA and serological reactions.

Considerable progress has thus been made in the understanding of the genetic-historical relationship among coffee species.

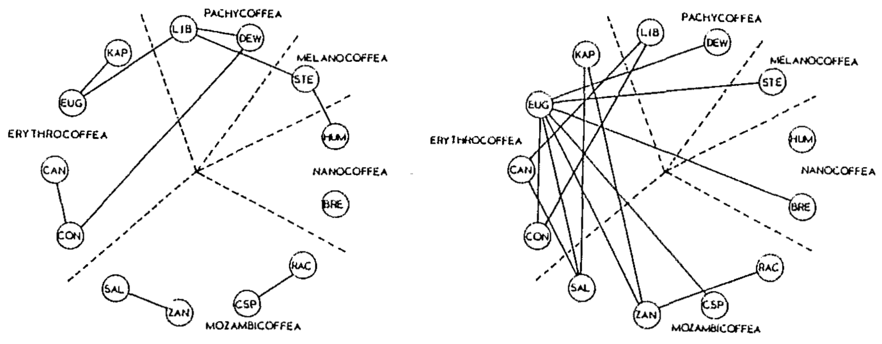
The Diploid Coffee Species

From the extensive cytogenetic studies on interspecific hybrids — a summary of the most relevant data together with major references is presented in Table 2.9 — the following main conclusions can be drawn as regards the genetic differentiation of the diploid coffee species

(1) Absolute crossing barriers appear to be absent within the genus *Coffea,* although considerable variation in the degree of successful hybridisation exists between species of different taxa.
(2) Exact quantitative information on the genetic relation of species is difficult to obtain due to the influence of genotype, crossing techniques and environment on the rate of success of interspecific hybridisation.
(3) Maternal effects can be very significant in crosses between species, which differ in the time interval between flowering and ripe fruits: the best results are usually obtained when the species with the quickest formation of the albumen is used as female parent.
(4) In general, crosses between species within one group present the least difficulty: for instance *C. canephora* and *C. congensis,* which both belong to the subsection *Erythrocoffea,* or species of the section *Mascarocoffea.* However, considerable success can sometimes be obtained as well with taxa of different taxonomic groups: for instance *C. liberica* and *C. eugenioides* or *C. dewevrei* and *C. stenophylla.* The species *Psilanthopsis kapakata* (erroneously classified in another genus by Chevalier) can easily be crossed with *C. canephora* and *C. eugenioides.*
(5) *C. eugenioides* performs in general much better in crosses with all other diploid taxa than *C. canephora.* This difference is particularly evident in crosses with species of the section *Mascarocoffea* (Figure 2.8)
(6) Intergeneric hybridisation between *Coffea* and *Psilanthus* has been unsuccessful so far.

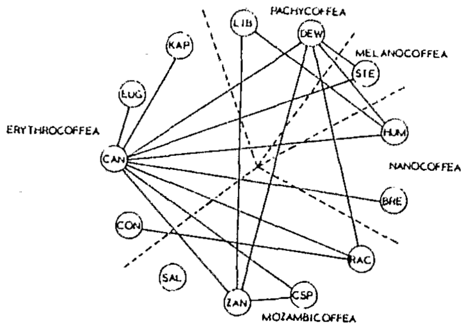
All diploid species of the genus *Coffea* have maintained a similar chromosomal structure, which would arise from the same basic A genome (monophyletic origin). Charrier (1978) observed a variable rate of PMCs

Figure 2.8: Genetic Relationships Between Species of *Coffea* (according to number of hybrids per 100 flowers). From Louarn, 1982 (1,2,3); Charrier, 1978 (4); Carvalho and Monaco, 1968 (5)

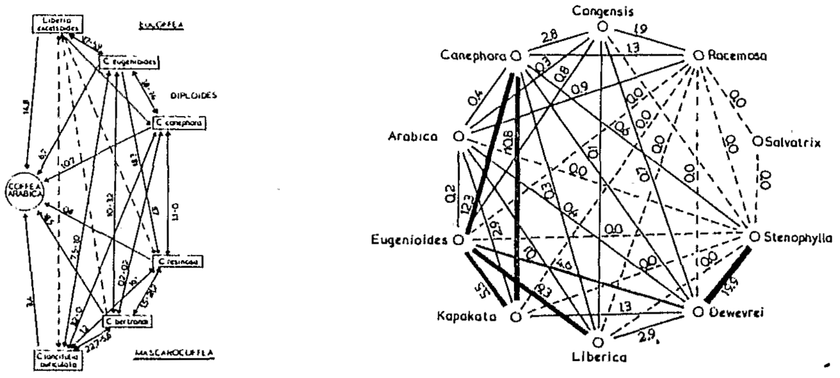


(1) More than 19 hybrids per 100 flowers

(2) 6-18 hybrids per 100 flowers



(3) Less than 5 hybrids per 100 flowers



(4)

(5)

(pollen mother cells) with 11 bivalents in F_1 hybrids between diploid species and found this to be highly correlated with fertility. It appears that all diploid coffee species have preserved the identity of their common origin during the evolutionary history notwithstanding the geographical isolation. This lack of chromosomal differentiation was also observed by Bouharmont (1959; 1963) in the caryotypes of ten African coffee species. An exception is the chromosomal aberrations found in hybrids between *C. kianjavatensis* and *C. canephora* (Lanaud, 1979). The genetic diversification of the diploid coffee species would therefore result essentially from genetic differentiation, which causes various levels of interspecific incongruity.

A good example of species which are morphologically and ecologically clearly distinct, but show almost normal chromosome pairing and good fertility in hybrids, are *C. canephora* (distribution in West and Central Africa) and *C. congensis* (limited to the banks and flooded islands of the Congo and Oubangui rivers). The latter species occupies a specific ecotype well isolated from the former by a very strict ecological barrier (Berthaud and Guillaumet, 1978). In the subsection *Pachycoffea* the exact position of *C. liberica sensu stricto* (berries with thick mesocarp) in relation to *C. dewevrei* (berries with thin mesocarp) is not yet clear. On the other hand, the abundant number of taxa in the section *Mascarocoffea* described by Leroy often correspond to allopatric populations with distinct morphological characteristics but nevertheless without strongly developed crossing barriers. Apparently, effective geographical isolation has produced genetically divergent populations through genetic drift and natural selection pressure. A similar situation could also be found in East African coffee species (Leroy, 1982; Hamon, Anthony and Le Pierrès, 1984). From a taxonomic point of view some taxa found in East Africa should not be classified as different species.

On the other hand, genetic divergence is in species like *C. canephora, C. liberica* and *C. eugenioides* exhibited as partial incongruity. For example, Louarn (1982) obtained fairly fertile F_1 hybrids between these three species, but their meiotic behaviour was characterised by a reduced pairing of the chromosomes (only 40-50 per cent of the PMCs had 11 bivalents). In addition there is a genetic effect on the chromosome pairing and the hybrid fertility within the interspecific combination *C. liberica* × *C. canephora* (Louarn, 1980). Similar genetic divergence appears to exist also between some series of *Mascarocoffea.*

There is a particularly sharp differentiation between *C. canephora* and the section *Mascarocoffea*: the rare F_1 hybrids obtained are weak and almost completely sterile. This genetic divergence is less pronounced for *C. eugenioides,* since crosses between this species and *Mascarocoffea* produces a higher proportion of fairly fertile F_1 hybrids.

It is in fact astonishing that a geographic isolation, started in the Upper Cretaceous, when Madagascar was separated from the main African continent, did not have a more profound effect on the chromosomal differentiation between coffee species. In this respect it is interesting to note the affinity of the Malagasy coffee species with East African coffee species (Charrier, 1978), in particular the similarity between *C. grevei* and *C. rhamnifolia* (ex *C. paolia*) (Leroy, 1980).

Little work has so far been done on the intergeneric relationship between *Coffea* and *Psilanthus.*

Cytogenetic Evidence for the Origin of Coffea arabica

C. arabica, the only tetraploid species in the genus *Coffea,* is indigenous to the highlands of south-western Ethiopia and south-eastern Sudan. The diploid meiotic behaviour and the fact that its centre of genetic diversity is situated outside the area of distribution of the diploid coffee species, indicate an allotetraploid origin (Carvalho, 1952). According to Grassias and Kammacher (1975), *C. arabica* has to be considered as a segmental allotetraploid.

C. eugenioides and *C. canephora* (or *C. liberica* or *C. congensis*) have often been assumed to be the ancestral parents of *C. arabica* (Carvalho, 1952; Cramer, 1957; Narasimhaswamy, 1962). However, meiotic pairing of chromosomes of the two genomes in interspecific hybrids of *C. eugenioides* and *C. canephora* was observed to be better (Louarn, 1976) than in dihaploid plants of *C. arabica* (Mendes and Bacchi, 1940; Berthaud, 1976). Besides, duplication of such interspecific hybrids (allodiploids) produces tetraploids with autotetraploid meiotic behaviour, such as the formation of quadrivalents. Louarn (personal communication) has observed this in different interspecific combinations.

Triploid hybrids, as a result of crosses between *C. arabica* and diploid species, show vigorous growth, but they are almost completely sterile as would be expected. Table 2.10 summarises the observations on meiotic behaviour of interspecific hybrids between *C. arabica* and different diploid coffee species made by various coffee geneticists. The number of bivalents plus trivalents formed during meiosis is, with few exceptions, close to 11. This would suggest that one genome of *C. arabica* has close affinity to the genome present in the diploid species, therefore that in the genus *Coffea* all species share the same basic genome and have a monophyletic origin.

C. arabica could have arisen from natural hybridisation between two ancestral diploid coffee species followed by unreduced gamete formation (see Demarly, 1975, for a description of the rare events that can lead to the occurrence of unreduced gametes). The degree of homology of the two genomes could have been high as a consequence of the monophyletic origin of the participating species, but various mechanisms (preferential pairing, genetic regulation of the synapsis) are likely to have played an

Table 2.10: Review of the Cytogenetic Behaviour of Interspecific Crosses Between *C. arabica* and Diploid *Coffea* Species

Triploid F_1 hybrids	Chromosome associations I	II	III	Others	PMC with 11 bivalents %	Pollen fertility %	References
C. arabica × *C. canephora*	14.4	5.4	2.60	—	—		Krug and Mendes (1940)
	7.80	9.75	1.61	0.21	89		Kammacher and Capot (1972)
	7.98	9.55	1.93	0.04			Chinnappa (1968)
	9.87	9.57	1.33	—	90	4	Louarn (unpublished)
C. arabica × *Liberio-excelsoides*	9.28	9.64	1.44	0.03	77	6	Charrier (1978)
C. arabica × *C. eugenioides*	9.70	9.64	1.34	—	92	7	Louarn (unpublished)
C. arabica × *C. kapakata*	10.07	9.45	1.33	—	62		Monaco and Medina (1965)
C. racemosa × *C. arabica*	11.3	9.7	0.80	—	49		Medina, 1963
C. arabica × *C. betrandi*	11.9	8.6	1.3	—	24	1	
C. arabica × *C. perrieri*	12.4	8.2	1.4	—	21	2	Charrier (1978)
C. arabica × *C. pervilleana*	14.3	8.6	0.5	—	10	1	
C. arabica × *C.* sp. A311	17.1	7.7	0.2	—	2	1	

important role in the progressive diploidisation from the archetype tetraploid to the present amphidiploid *C. arabica.*

Lobreau-Callen and Leroy (1980) observed in their palynological studies that *C. arabica* produces two types of pollen: one type related to *C. canephora* and one closely resembling pollen of *C. rhamnifolia,* a xerophytic species indigenous to the coastal regions of Somalia and Kenya. This would not necessarily contradict the foregoing cytogenetic evidence, but a definite conclusion on the origin of *C. arabica* will have to await further studies, including the intergeneric level between *Coffea* and *Psilanthus.*

Biochemical and Serological Affinities in Coffea

Enzyme Polymorphism. Studies on enzyme polymorphism in *Coffea* started with Payne and Fair-Brothers (1976), who compared total crude proteins and malate dehydrogenase in seeds of *C. arabica* and *C. canephora,* and Guedes and Rodrigues (1974), who studied the phenoloxidase variability after polyacrylamide electrophoresis of extracts taken from genotypes of *C. arabica,* used as differentials for the identification of physiological races of leaf rust (*Hemileia vastatrix*).

Methods of analysing enzyme polymorphism have been further developed to study the genetic affinities between various coffee populations by Berthou and Trouslot (1977) and Berthou *et al.* (1980) in Ivory Coast. The horizontal starch-gel electrophoresis technique was applied initially to three and later to eight enzyme systems and this led to the identification of a number of loci. Allozymatic frequencies were estimated for natural coffee populations. Estimates of genetic distances between species, whereby an index developed by Nei (1972) for 3-8 enzyme systems was used, gave the following information:

(1) *C. canephora* and *C. congensis* have the same allozymes with different frequencies; the genetic distance between the species is larger than between populations of the same species: the Nana taxon is therefore clearly to be considered as part of *C. canephora.*
(2) The genetic distance between *C. liberica* from Ivory Coast and *C. dewevrei* from the Central African Republic is of the same order as that between *C. liberica* and *C. humilis* from Ivory Coast. This evidence justifies a clear distinction between *C. liberica* and *C. dewevrei,* which both belong to the subsection *Pachycoffea.*
(3) The genetic distances between the species *C. canephora, C. liberica* and *C. eugenioides* are considerable.
(4) The enzymic affinities of *C. arabica* with all different diploid coffee species are similar. According to Berthou and Trouslot (1977) *C. arabica* would result from the complementary electrophoretic bands of acid phosphatases and esterases of *C. eugenioides* and *C. canephora* or *C. congensis.*

(5) Lower enzymic affinities have been found between species of the genus *Coffea* and the genus *Psilanthus* such as *Paracoffea ebracteolata.*

Cytoplasmic DNA. Berthou *et al.* (1980, 1983) have applied methods of identifying DNA of cytoplasmic organelles (chloroplasts and mitochondria) to coffee. Such methods include separation by electrophoresis on agarose slab gels of fragments of DNA obtained by bacterial restriction enzymes.

Electrophoresis of fragments of chloroplast DNA, obtained by the Hpa II enzyme (from *Haemophilus parainfluenzae*) suggest that the following species have a similar origin: *C. arabica* and *C. eugenioides*; *C. canephora*, the Nana taxon and *C. congensis*

Electrophoresis of fragments of mitochondrial DNA, obtained by action of the Sal I enzyme (from *Streptomyces albus*), suggested the following affinities: (a) great similarity between *C. canephora* and the Nana taxon; (b) great similarity of *C. arabica* with *C. eugenioides* and *C. congensis*; (c) considerable divergence between *C. canephora* and *C. arabica* or *C. eugenioides*; (d) wide genetic divergence between *C. dewevrei* and *C. liberica* and *Paracoffea ebracteolata*

Evidently, electrophoresis of mitochondrial DNA confirms the distinction between the subsections *Abyssinicae* (*C. arabica, C. eugenioides* and *C. congensis*) and *Robustae* ((*C. canephora*) earlier proposed by Lebrun (1941). The affinity of *C. canephora* with *C. congensis*, as indicated by the similarity of chloroplast DNA is clear, but these two species show differences in their mitochondrial DNA. This type of analysis has also indicated that the Nana taxon should be considered as an ecotype of *C. canephora.*

Serological Affinities. Antisera obtained for *C. arabica* and *C. canephora* were used in serological reactions with soluble antigens from seed of various coffee species (Hofling and Oliveira, 1981). It was possible to establish the following relationship: *C. arabica* has more affinity with *C. congensis and C. eugenioides* than with *C. canephora.*

Other Chemical Affinities. Chromatographic analysis of the flavonoid component (Longo, 1975) indicated that *Psilanthopsis kapakata* belongs to the genus *Coffea* rather than *Psilanthus* as earlier proposed by Chevalier.

Additional data, based on simple chemical tests applied by Ram, Sreenivason and Vishveshwara (1982), suggest that *C. eugenioides, C. racemosa* and *P. kapakata* are more closely related to each other than to *C. salvatrix.* Nevertheless, all four species are rightly classified under the subsection *Mozambicoffea* (see also Chapter 13: 334).

Conclusions

From this review of advances in the taxonomy and botany of coffee the following main conclusions can be drawn.

(1) A general revision of coffee taxonomy should take into account the new insights into the relationships of coffee species, acquired by the extensive exploration of natural habitats and centres of high genetic diversity, as well as by the application of modern concepts of the biological series and of biosystematic classification systems.

(2) During the evolutionary organisation of the coffee gene pool differentiation into species was not accompanied by the development of strong crossing barriers. This offers considerable prospects for introgressing desirable characters into cultivated species or the development of new cultivars by interspecific hybridisation. Of particular interest are the taxonomic affinity of *C. congensis* and *C. canephora* (Congusta hybrids) and the crossability of *C. eugenioides* with many other diploid species. There are also indications that *C. eugenioides, C. congensis, C. canephora* and the allotetraploid *C. arabica* have originated from common ancestral forms.

(3) There is a great urgency for intensifying studies of the still existent wild coffee populations, especially in those geographic areas where such populations are most threatened by extinction. The preservation of this coffee germplasm should be secured, either by conservation of the natural forest habitats or by establishing living collections. The following regions require special attention in this respect:

— The highlands of south-western Ethiopia and south-eastern Sudan (Boma Plateau): the centre of high genetic diversity for *C. arabica*;

— Uganda and Central Africa (Gabon, Congo, Zaire): the major areas of distribution for many diploid coffee species;

— The Malagasy Republic: the centre of genetic diversity for species of the section *Mascarocoffea.*

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