FOOD FOR THOUGHT

GENETIC, HISTORICAL AND ETHNOBOTANICAL STUDIES OF TARO *Colocasia esculenta* (L.) SCHOTT IN AFRICA

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ABSTRACT

The presence of exotic plants both in Africa and in Asia has long attracted the attention of scholars who have attempted to understand the human activities linked to them. Archaeological and ethnographic evidence for the reconstruction of these activities is often very limited, but indirect methods such as the study of DNA have become useful tools in building models of early human dispersal. Among the plants that were carried across the Indian Ocean, sometimes known as the "tropical food kit", the staple crop taro (*Colocasia esculenta* (L.) Schott) has continued to be the subject of ongoing research. The use of this crop in antiquity is well documented by discoveries of ancient taro starch granules found on archaeological artefacts from sites in Southeast Asia and the Pacific islands, making it one of the oldest plants consumed by people. However, less is known about the use of taro in Africa and the Mediterranean region, where it is found both in the wild and under cultivation - often representing a staple crop in Sub-Saharan Africa. In this doctoral thesis, genetic analysis was performed on modern samples of taro collected from Africa and other regions of the Indian Ocean, using four molecular markers. Two main clusters have been identified, and within this main sub-division four populations of taro have been detected in Africa. By integrating the genetic results with historical and linguistic research, and extensive ethnobotanical fieldwork in Africa, two of these populations are proposed to represent early translocations, with modern distribution patterns suggesting diverse dispersal routes at different times. These results open up a new scenario in which the "tropical food kit" is finally unpacked, with important historical implications for each of the crops contained within it.

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CHAPTER 1 INTRODUCTION

The study of complex cultural history necessarily involves a multidisciplinary approach. This is particularly true when historical information is lacking, with the combination of several disciplines having great potential to unravel controversial and complex issues. Archaeological research is a prime example of the application of diverse approaches, which individually may shed only limited light on specific aspects, but when combined may be much more revealing. In this context, the geographical distribution and genetic characterization of living plants has becoming increasingly important in studies of crop movements carried out by human agency (Gunn et al., 2011; Perrier et al., 2011; Trejo et al., 2012; Trudgen et al., 2012; Roullier et al., 2013). The data stored in genetic code contains information about past evolutionary events, and when its analysis is combined with the study of geographical patterns and ethnobotany, useful insights can be gained.

This doctoral dissertation deals with early human movements and crop translocation within Africa and between Africa and Asia, focusing primarily on the genetics, history and ethnobotany of taro (*Colocasia esculenta* (L.) Schott) located in Africa. This piece of research is part of the broader Sealinks Project.

Its aim is to increase understanding of early human activities in the region of the Indian Ocean, focusing in particular on the last millennium BC and the first millennium AD. The project is interdisciplinary in nature and combines the expertise of researchers who work together to increase understanding in this area, making use of a broad range of disciplines, including archaeology, archaeobotany, anthropology, linguistics, and molecular genetics to explore the origins and development of early exchange and connectivity in the Indian Ocean. The project is characterized by research that involves the study of discrete topics, including five different sub-projects, each focusing on a particular area. Two of these sub-projects examine specific prehistoric communities of the Indian Ocean rim and their relationships with the wider Indian Ocean world, with the other three being the subject of doctoral research involving targeted investigations of specific linguistic and genetic issues. The research addressed in this thesis focuses on the dispersal of a crop species across the Indian Ocean, into Africa and also from the perspective of the Mediterranean world. Specifically, it makes use of the history and genetic features of taro to attempt to understand its dispersal from Asia to Africa and within the African continent. The research draws from three different approaches: genetic analysis of samples collected in Africa and in other parts of Asia, historical literature, and ethnobotanical observations.

HYPOTHESES FOR THE INTRODUCTION OF TARO TO AFRICA

Taro is a tropical plant native to Asia (De Candolle, 1883; Engler and Krause, 1920; Burkill, 1935) and it is now cultivated in Africa, where it is a staple (Ofori, 2003) and a resource in small-scale farming (Shange, 2004). In the Pacific region, it is known to have been in use in Papua New Guinea since the early Holocene (Denham et al., 2003; Fullagar et al., 2006), with the retrieval of starch grains found on archaeological sites in the Solomon Islands (Loy et al., 1992) and Borneo (Barton and Paz, 2007) suggesting potential exploitation of taro since the Pleistocene.

A range of Asian crops in Africa have been the focus of study by archaeologists (e.g., Neumann and Hildebrand, 2009; Mbida et al., 2000; 2001; Lejju et al., 2006), historians (Wigboldus, 1994), plant scientists (De Langhe, 1994), geneticists (Lebot et al., 1998; Perrier et al., 2011) and linguists (Blench, 2009; Beaujard, 2011) in an effort to improve understanding of crop movements between the two continents. The question of how and when taro arrived in Africa has attracted the attention of many scholars for over a century (e.g., De Candolle, 1883; Burkill, 1935; Täckholm and Drar, 1941; Portères, 1960; Williamson, 1970; Blench, 1996; Van der Veen and Morales, 2011), but limited historical data, sparse ethnobotanical information and a scarcity of genetic research on this plant in Africa have so far hampered the reconstruction of its routes of dispersal.

Historically, three main hypotheses have been put forward to explain the introduction of taro to Africa, and in this research they have been tested with the aim of discarding, accepting or improving one or more models of translocation.

The first hypothesis postulates that around the beginning of the Christian era (Reinhardt, 1911 cited in Rivers, 1914: 273; Burkill, 1935; Plucknett, 1970; 1976) or during the Islamic period (Watson, 1983) taro entered Africa via the Nile valley, from which it subsequently spread across the continent. This hypothesis is based on references from classical sources, with the Greek word *colocasia* a central tenet for the arguments. Whether or not the *colocasia* of Greek and Roman authors was indeed taro has been debated in the Italian literature since the Renaissance (Anguillara, 1561; Matthioli, 1565; Alpini, 1592). Chapter 6 entitled "Taro in the Mediterranean world" will review this topic in detail.

The second hypothesis implies an introduction of this plant from India or Sri Lanka into the Arabic world (De Candolle, 1883), and/or from Southeast Asia into East Africa (Murdock, 1959). This could be referred to as the "sea-borne hypothesis". Murdock saw Austronesian seafarers as responsible for carrying taro from Borneo via Madagascar during the 5-7th century AD. Following this introduction of the plant, he suggested that Iron Age farmers eventually spread it across the rest of Africa. Murdock put forward this hypothesis after having observed the presence of Asian crops in Africa,

among which taro, banana (*Musa x paradisiaca* (L.) Colla) and water yam (*Dioscorea alata* L.), played a significant economic role.

The third, and probably most contentious hypothesis proposes that Indonesian people, sailing westwards, may have arrived in Madagascar and then navigated around the Cape of Good Hope to reach the West African coasts where they then introduced the crop (Jones, 1971). Similarities between musical instruments in West Africa and Indonesia lend support to this idea, which led Jones to link these two distant regions. His hypothesis has been much criticised by Blench (1982, 1996), who concluded that problematic methodology and misinterpretation of data had led Jones to erroneous conclusions. He argues that the hypothesis was based solely on the comparison of material culture, which on its own would not be sufficient to make a case for cultural connections (Blench, 1982). These contentions aside, the diversity of names for taro in West Africa (Burkill, 1988) has highlighted the need to conduct genetic research on plant material present in this area.

So far, archaeobotanical research has not been sufficient to favour any particular scenario for the introduction of taro to Africa. The only archaeobotanical finds of taro in the continent are the macroremains of taro corms retrieved at Quseir al-Qadim, in Egypt, dated 1070 cal BP (Van der Veen and Hamilton, 2011, Appendix 1; Van der Veen and Morales, 2011). It is hoped that genetic study may shed more light on the matter, and this thesis constitutes an initial step in this direction. These various hypotheses will be

taken into account when exploring the implications of the multidisciplinary dataset collected and studied by the author.

AIMS AND RESEARCH QUESTIONS OF THIS STUDY

The rationale behind this project is to use the genetics, history and ethnobotany of taro to provide insights into its entry and distribution in Africa. In particular, the key aims that were set for this research were:

1. To use the genetics of taro to shed light on early human activities in the Indian Ocean; and

2. To improve knowledge on taro in Africa through study of its genetics, history, and ethnobotany.

More specifically, this thesis will examine five main research questions:

1) What can we learn about the history of taro both in and outside Africa from genetic variation in the crop?

2) What can we learn about the history of taro from local names in Africa and beyond?

3) What are the uses and the processing methods of taro in Africa? Can these be related to wider culinary or culture-historical trends or areas?

4) What are the most likely points and routes of introduction of taro into Africa?

5) What are the implications for maritime movements of the plant and people and/or for trade/exchange patterns?

The objectives are:

1) The analysis of the genetic pattern of taro populations in Africa.
2) Genetic investigation of the taro corm retrieved at Quseir al-Qadim.
3) To improve ethnobotanical knowledge of taro in selected African countries.
4) A review of the historical material linked to taro in the Mediterranean world.

DISSERTATION STRUCTURE

This work will be presented according to the following structure:

In chapter 2 a review of the existing literature on taro in Africa will be presented. Two maps will accompany this discussion. The first one is a map that shows the historical presence of taro in Africa, which was created by the author from the literature, floristic records, academic papers and agronomic reports. The second map shows the countries where taro has been cultivated, based on data gathered from the Statistics Division of the Food and Agriculture Organisation (FAO) from the years 1961 to 2011.

Chapter 3 addresses the material and methodology used for the genetic characterisation of taro. The material collected during fieldwork and received from third parties will be presented here, accompanied by a map that shows the locations from where taro was collected. This will be followed by a presentation of relevant studies which have previously been conducted on taro. Finally the genomic regions chosen for the genetic study will be outlined.

In Chapter 4 the outcomes of three months of fieldwork which was conducted by the author in four Africa countries will be presented. In particular, ethnobotanical observations of taro gathered in the Democratic Republic of Congo, Cameroon, Kenya and Tanzania will be examined. Relevant illustrations demonstrating the morphological diversity observed in taro in these countries will accompany the discussion.

In Chapter 5 the results of the genetic analyses will be presented. Firstly, the description of chloroplast variation of African taro samples will be presented with comparisons to the work conducted by Ibrar Ahmed at the Massey University, New Zealand, towards a wider discussion of the chloroplast. Secondly, the nuclear variation of selected regions will be presented, together with the analyses performed and results achieved.

In Chapter 6, the literature on taro and its overall presence in the Mediterranean area will be presented and discussed. In this chapter, selected words and texts in the Greek, Latin, Arabic, Medieval and Renaissance

literature will be examined. A map of the presence of taro in the Mediterranean has been produced to accompany this text and discussion.

In Chapter 7, the observations and results will be synthesised and discussed in the light of the picture obtained, and the most likely hypothesis for the introduction of taro in Africa will be presented.

Finally, in Chapter 8 the conclusions of this research and the usefulness of the data extracted will be summarised in the context of the original research objectives and goals of the dissertation.

CHAPTER 2 LITERATURE REVIEW ON TARO IN AFRICA

INTRODUCTION

The use of plants as a proxy for the reconstruction of human activities, through migration, agricultural expansion, trade or simple regional interactions cannot be viewed as an uncomplicated process. This is especially true for old crops such as taro where its natural range encompasses large and diverse geographical regions (Matthews, 1991), and where domestication events are as yet to be fully understood (Ahmed et al., 2013). The use of crops as proxies should therefore be analysed as a complex history with its own dynamics linked to dispersal, trade and other forms of exchange and mobility. However, while a single crop cannot comprehensively explain human dynamics, a detailed analysis can provide clues about local uses and regional interactions. It can, therefore, become a partial proxy for the expansion of agriculture and an indicator of human life ways.

In researching human activities and the dispersal of crop species across the Indian Ocean, the case for using taro is a convincing one. This crop represents a staple in some African countries (Ofori, 2003; Shange, 2004; Mare, 2006), and its antiquity in this continent is attested since the 10th century AD (al-Masudi, 1864). There has been a paucity of information available on its genetics, but now questions of how and when this crop was introduced into

Africa with the benefit of new research in this area is encouraging further study to help reconstruct human movements and crop dispersal across the Indian Ocean and the African continent.

In the next section I am going to introduce African crops that were found in Neolithic sites in Asia. They are important in terms of early translocations and by implication, human agency.

EARLY EXCHANGES BETWEEN AFRICA AND INDIA

The discovery of crops of African origin at Neolithic and Bronze Age sites in Pakistan and India has created much research interest in how and when these plants were moved, and which routes they followed in their translocations (e.g. Harlan, 1976; Weber, 1998; Blench, 2003; Fuller, 2003; Mitchell, 2005; Boivin and Fuller, 2009; Fuller and Boivin, 2009). Apart from various minor plants which moved out of Africa (Blench, 2003) at a time as yet unknown, the 'big five' (Fuller and Boivin, 2009) which have created most of the interest for archaeobotanists are sorghum (*Sorghum bicolor* (L.) Moench), pearl millet (*Pennisetum glaucum* (L.) R. Br.), finger millet (*Eleusine coracana* (L.) Gaertn.), cowpea (*Vigna unguiculata* (L.) Walp.) and lablab (*Lablab purpureus* (L.) Sweet). Tamarind (*Tamarindus indica* L.), which, despite is species name suggesting otherwise, is of African origin (Diallo et al., 2007), and appeared later in Asia.

While initial arguments put forward the hypothesis of an "African package" of plants arriving together in South Asia, subsequent archaeological investigations and genetic studies do not support this, leaving the matter of how these crops arrived in Asia requiring further research. Previously, questionable dating and ambiguous identification also raised doubts about the archaeobotanical reliability of the translocations (Blench, 2003). Fuller, however, provided a critical evaluation of material originating from Indian sites (Fuller, 2003), and argued that while a number of reports were dubious, there are nonetheless numerous well-identified African crops in secure, dated archaeological contexts in South Asia (see also Boivin and Fuller, 2009).

The early dates and great morphological variation associated with this archaeobotanical material had originally led scholars to consider these crops as Asian domesticates (Vavilov, 1951). However, based on the distribution of wild plant types, sub-Saharan Africa has been identified as the centre of origin of sorghum (Dogget and Rao, 1995) and pearl millet (Brunken et al., 1977). In fact, these crops are largely cultivated in the African savannah, where they represent the principal source of food for people who live in these regions (FAO, 1995).

The presence of these crops in the Indian sub-continent therefore indicates that people were moving between Africa and India by the second millennium BC if not earlier (Boivin and Fuller, 2009). The low abundance of these crops on early South Asian sites suggests that they were minor crops at

that time, and that they were used as an addition to the indigenous cultivation system (Weber, 1998; Fuller, 2003; Boivin and Fuller, 2009; Fuller and Boivin, 2009).

Burkill (1937: 118) was one of the first authors to hypothesise that sorghum had reached India in prehistory. However, the dearth of early, reliable archaeobotanical finds of African crops on the Arabian peninsula has promoted the idea of transmission by sea rather than by land (Blench, 2003; Boivin and Fuller, 2009). Similarly, having clear African origins (Portères, 1976: 433) and no intermediate archaeological examples, pearl millet presents an analogous case along with sorghum, in which the absence of material in Egypt, the Near East and Arabia indicates the use of a sea-route rather than a land-route.

Tamarind, which is indigenous to the dry African savannah, is also considered to have reached Sri Lanka in prehistory (El-Siddig et al., 2006). A more recent introduction has been proposed by Shah (2013), who has linked the Ethiopian vernacular name *hommar* and *tommar* on the basis of logical similarities, suggesting that Ethiopian merchants could have introduced this plant to Sri Lanka and India during the early part of the first millennium AD.

In the past, Burkill (1938) and subsequently Murdock (1959) described the so-called 'Sabaean Lane', a shipping route passing from the Malabar coasts via South Arabia to the Horn of Africa, thus indicating a path for the transmission of food crops from India to East Africa. This route implies the

need for monsoon winds and ocean currents to enable navigation of the waters of the Indian Ocean, sailing from Africa to India following the summer monsoon, with the winter counter current being used for the return journey (Schott and McCreary, 2001) (Figure 1).

Figure 1. Sabaean Lane (Source: Collins and McDonald Burns, 2007: 98).

In this respect, the ancient Greek document, *The Periplus of the Erythraen Sea*, supports the existence of a trade network along the ocean coasts. This is a document written during the first century AD by a Greek-speaking Egyptian (Schoff, 1912) who listed ports, people and commodities at locations along the Red Sea, the coasts of East Africa, the Arabian Peninsula and along the Indian and Sri Lankan coasts into the Bay of Bengal (Casson, 1989). The Periplus also describes trans-oceanic routes, which drew on the power and seasonality of

the monsoon winds to enable direct voyaging between the Red Sea and south India, beginning at the end of the first millennium BC (Casson, 1989).

The use of sea vessels would also help to explain the dispersal of commensal species around the Indian Ocean, some from or via the Indian sub-continent. The close association between humans and commensal species has been drawn upon using genetic diversity patterns to provide insights into human movements (Matisoo-Smith and Robins, 2004; Jones et al., 2013). This possibility has been confirmed by the analyses of DNA variation of such commensals, which have provided strong evidence that these biological vectors are useful tools for understanding prehistoric human mobility (Matisoo-Smith and Robins, 2004). Likewise, animals that have adapted to human environments, such as house mice (*Mus* spp.), rats (*Rattus rattus*), and sparrows (*Passer domesticus*) have great potential to help analyse human activities. For example, in a recent study, the phylogeography of house rats was used to explore patterns of human migration in the western Indian Ocean (Tollenaere et al., 2010). The house rat, also known as the black rat (*Rattus rattus*), originated in Southeast Asia and later spread worldwide, with this study showing how a human dispersal model could be linked to its introduction into Madagascar in ancient times.

Zebu (*Bos indicus* L.) also originated in South Asia and its genetics have been used as a proxy to infer early human movements and/or trade between India and Africa. Genetic patterns of zebu introgression into Near Eastern,

Arabian and African cattle suggest a pattern of predominantly maritime translocation (Hanotte et al., 2002; Zeder, 2006; Boivin and Fuller, 2009; Fuller and Boivin, 2009). Summing up, there is therefore, a body of evidence which supports the contention that in ancient times the Indian Ocean acted as a seascape for the development of the first transcontinental trades, linking Africa, South Asia and other regions.

ASIAN CROPS IN AFRICA, THE POSITION OF TARO IN THE 'TROPICAL FOOD KIT'

The story of the translocation of Asian crops now found in Africa is less clear, with much more limited archaeobotanical data available. Routes of translocation directly from Southeast Asia, via India, perhaps by the Sabaean Lane, or as a result of Medieval Islamic trade are all proposed. Clearly, these notions represent quite different seafaring strategies, chronologies and mechanisms.

George Peter Murdock was one of the first scholars to point out the presence of Asian crops in Africa. In his book *Africa: Its People and Culture* (1959), Murdock attempted to reconstruct African culture history, including the early development of agriculture in the continent. Though ethnographically questionable in many respects (Asiwaju, 1985: 254; Blench, 1996), his work was important in bringing to the attention of the research

community the question of how various exotic crops were introduced to Africa. In examining this question, he explored geographical crop patterns, described local uses and suggested a model of the dispersal of crops that he grouped according to their place of origin. Among the plants that reached East Africa, Murdock (1959: 206-08) categorised cultivated plants of Indian origin which he named the *Indian complex* (Table 1), and those of Southeast Asia origin that he labelled the *Malaysian complex* (Table 2), which included taro.

Table 1. Indian complex identified by Murdock (1959: 206-7).

Legumes	Leaf and Stalk vegetables	Vine and Ground fruits	Tree fruits	Condiments and indulgents
Mung bean *Vigna radiata* (L.) R.Wilczek	Jew's mallow (*Corchorus olitorius* L.)	Cucumber (*Cucumis sativus* L.)	Balsam pear (*Momordica charantia* L.)	Ginger (*Zingiber officinale* Roscoe)
Pigeon pea (*Cajanus cajan* L.) Millsp.		Eggplant (*Solanum melongena* L.)	Mango (*Mangifera indica* L.)	Hemp (*Cannabis sativa* L.)
Sword pea (*Canavaliaensi formis* (L.) DC.				

Table 2. Malaysian complex identified by Murdock (1959: 207-8).

Cereals	Tuber and root crops	Tree fruits and nuts	Condiments and indulgents
Rice (*Oryza sativa* L.)	Polynesian arrowroot (*Tacca leontopetaloides* (L.) Kuntze),	Banana (*Musa x paradisiaca* L.)	Areca palm (*Areca catechu* L.)
	Taro (*Colocasia esculenta* (L.) Schott)	Breadfruit (*Artocarpus altilis* (Parkinson ex F.A.Zorn) Fosberg)	Betel (*Piper betle* L.)
	Yam (*Dioscorea alata* L., *D. bulbifera* L., and *D. esculenta* (Lour.) Burkill)	Coconut palm (*Cocos nucifera* L.)	Sugarcane (*Saccharum officinarum* L.)

In the Indian Complex, Murdock also included the hyacinth bean, although he noted that some scholars considered it native to Africa. In fact,

this plant probably originated in Ethiopia (Verdcourt, 1971), and is certainly African (Boivin and Fuller, 2009; Fuller and Boivin, 2009). In assessing linguistic and ethnographic approaches, Murdock suggested that the Malaysian Complex was introduced by the Malaysian people to the east coast of continental Africa via the Sabaean Lane at some time between the second and the fourth centuries AD (1959: 208). He suggested that Malaysian people brought these crops by sea, and that once they had landed on the African coast, would have encountered "Megalithic Cushites", a population of Bushmanoid hunters-gatherers that occupied all of East Africa from western Ethiopia and the Eastern Horn south to the Cape of Good Hope.

Roger Blench (1996) renamed the Malaysian complex the *tropical food kit*, referring in particular to three starch crops: banana (both plantain *Musa x paradisiaca* L. AAB or ABB, and sweet banana *Musa acuminata* Colla AA or AAA), water yam (*Dioscorea alata* L.) and taro (*Colocasia esculenta* (L.) Schott). These crops are of Asian origin and according to their agronomical features, they are found in the humid tropical forests in the Equatorial belt, although each of them has its own distribution pattern (Harris, 1967). Several authors (e.g. Burkill, 1937; Plucknett, 1970, Purseglove, 1976; Wigboldus, 1994; Blench, 2009) have explored ideas concerning the way that these plants were introduced into the African continent, but their dispersal history has yet to be established.

Banana is one of the most frequently cultivated crops in modern Africa, which is testimony to its long-term impact on tropical rainforest agriculture, and has resulted in being the component of the tropical food kit that has received most attention (e.g. Simmonds, 1962; De Langhe et al., 2009; Blench, 2009). The genus *Musa* covers two different plant types, those with 20 chromosomes 2n=2x=20, which are inscribed in the sections Australimusa and Callimusa, and those with 22 chromosomes 2n=2x=22 which are in the sections Eumusa and Rhodochlamys. Eumusa is the section which contains most of the edible banana cultivars, with diploid and triploid forms deriving from *Musa acuminata* (A genome) and triploid cultivars *Musa balbisiana* (B-genome). A recent multidisciplinary study of banana has greatly improved understanding of the history of its domestication, the results showing that after hybridisation of AA forms of *Musa acuminata* occurred in Southeast Asia, triploids arose by intentional or accidental germplasm exchange carried out by people who were moving banana plants in the Southeast Asia region and New Guinea (Perrier et al., 2011). In Africa, an interesting distribution pattern of diploid and triploid forms suggests old connections with Southeast Asia that are yet to be resolved. On the Swahili coast and nearby islands (Zanzibar, Comoros, Madagascar) the cultivation of diploid AA cultivars of the *Mlali* subgroup is linked to their ancestral group, which probably originated in the southern region of the Southeast Asian area. Since East Africa is the only area where this group occurs outside Southeast Asia, an old maritime connection

has been suggested (Simmonds, 1962; Perrier et al., 2011). Similarly, the triploid hybrids AAA of the *Mutika Lujugira* subgroup are found only in the East Africa Highlands and are used for cooking and producing beer. This group is likely to have arisen from the fusion of diploid and haplotype gametes A (D'Hont et al., 2000).

In West Africa, African plantains with the genetic profile AAB group are identified in the group *banskii*, for which the probable place of origin lies in the area of the Philippines and New Guinea (Perrier et al., 2011). Evidence for the presence of African plantain in West Africa has always been problematic, and for a long time it had been thought that they had been introduced by the Portuguese (De Langhe et al., 1994). Linguistic studies associated with African plantain point to the arrival of the ABB group around 3000 cal BP (Vansina, 1990), suggesting an old introduction. Archaeobotanical retrieval of banana phytoliths at Nkang in Cameroon dated to the second half of first millennium BC (Mbida et al., 2001) is in line with this assertion. However, the question of how the plantain arrived in West Africa has yet to be resolved. Plantains are not extensively represented in East Africa (De Langhe et al., 2009), and their cultivation is quite rare in Asia (Sharrock and Frison, 1999).

Two different introductions have been proposed for African plantain and banana groups, in which extensive human movement, long distance contacts and trade would have been involved (Perrier et al., 2011). To date,

however, the lack of seeds and the difficulties of studying starchy crops in the archaeobotanial record have hampered a full reconstruction of the history of the banana complex, as well as their translocation to Africa. The retrieval of banana phytoliths dating to ca. 4000 years ago in Pakistan (Fuller and Madella, 2009) is intriguing, but its value as evidence is limited since this represents only a single findspot in the region, with associated linguistic data pointing to a much later presence of the crop (ibid.).

Water yam (*Dioscorea alata* L.) is the other key element in the tropical food kit. Genetic studies revealed that its centre of diversity is located in Melanesia (Lebot et al., 1998), but the question of how it reached Africa is still unresolved. The main difficulty with this crop is that distribution data are rare as scholars often confuse it with other native yams (Blench, 2007). Water yam is cultivated along with other native yams in the 'Yam Belt' in West Africa, and is also present in Ethiopia, East Africa and Madagascar, although it is less frequent in these areas (Blench, 2007). When the French visited Madagascar in the 17th century, water yam was already present (Lebot, 2009: 187; Beaujard, 2011), with linguistic studies suggesting that the first Malagasy settlers brought it with them in their westward expansion (Beaujard, 2011). It is not clear whether water yam was present when the Portuguese arrived on the coasts of West Africa, as they used collective names for different crops (Carney and Rosomoff, 2009: 103). However, Portuguese travellers could have

been responsible for the translocation of the plant across the Indian Ocean as provisions for shipping crews (Lebot, 2009: 188).

A GEOGRAPHICAL APPRAISAL OF TARO IN AFRICA

Of all the Malaysian crops that reached Africa in antiquity, it is taro that has received the least attention of plant genetic studies in Africa, with ethnobotanical research likewise receiving very limited coverage in the literature (e.g. Ofori, 2003; Shanghe, 2004; Modi, 2003; Fujimoto, 2009; Lewu et al., 2009).

Taro is currently a staple food in Nigeria, Cameroon, and Ghana, and although not extensively cultivated elsewhere, it also has a significant cultural role in the Democratic Republic of Congo, Ethiopia, Kenya, and Madagascar, with its importance as a food crop increasing during periods of famine. A map which shows the presence of taro in Africa has been drawn to better visualise its distribution (Figure 2), based on records and information found in floristic, agronomic reports, and academic papers. Many of the sources consulted are flora descriptions that were compiled during the colonial period; the reader should therefore note that the names of the regions have been often substituted with their modern designations. Appendix 1 at the end of this work reports all the sources from which data were extracted.

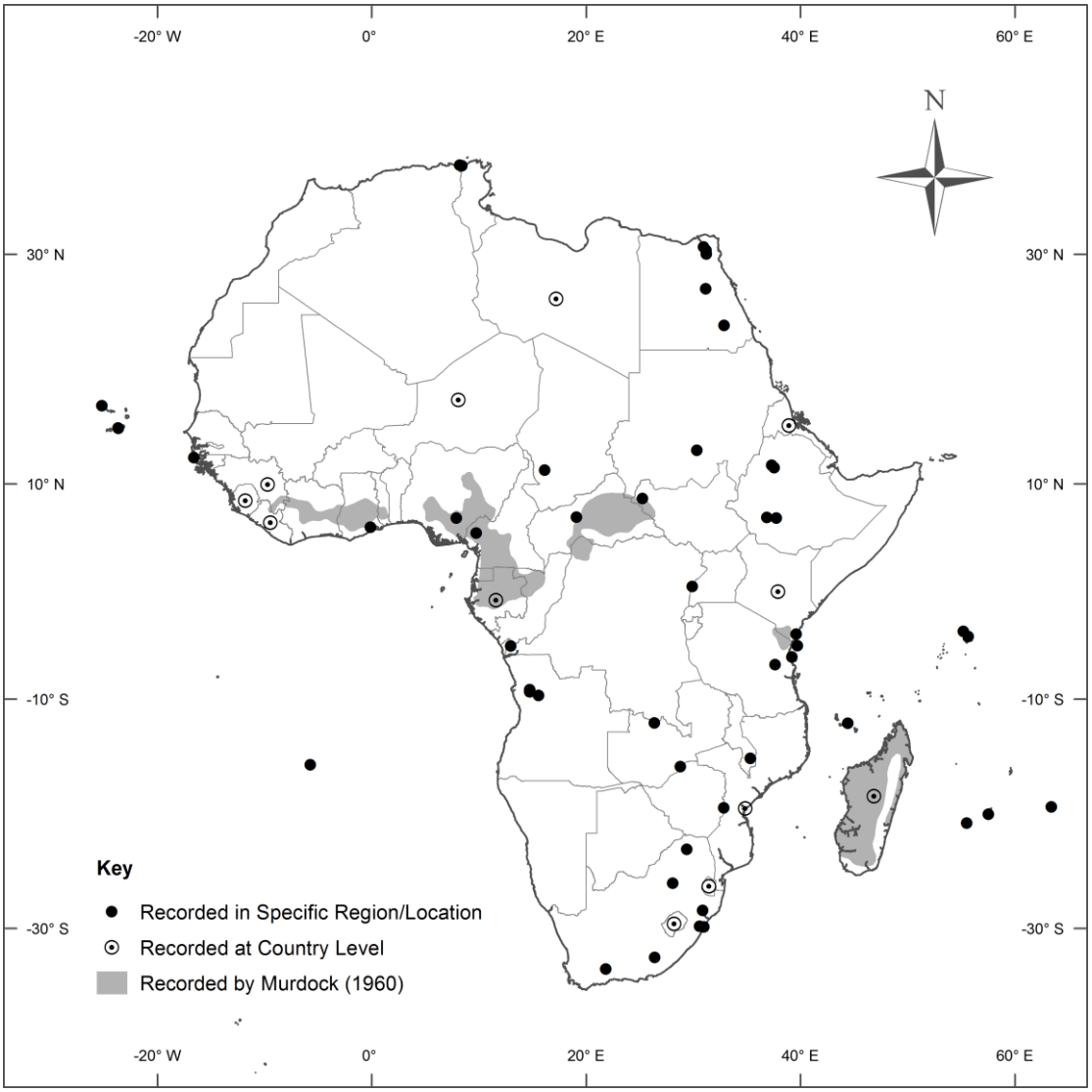


Figure 2. Historic map (1849-2012) of taro based on sources listed in Appendix 1 at the end of this work. Black circles indicate specific locations or areas in which the plant was recorded. Open dot circles indicate that the plant was recorded at country level without giving specific locations. Areas coloured in grey represent the regions specified by Murdock, 1960.

This map shows the collation of information on taro at country level as well as in specific locations. A distribution map of taro drawn by Murdock in 1960 has also been overlapped with these data. This is shown by the grey coloured area. Murdock's data refer only to *Colocasia esculenta* and not to the New World aroid *Xanthosoma sagittifolium* (Murdock, 1960).

Another map was also drawn using data collected by the Statistic Department of the Food and Agriculture Organization of the United Nations, FAO (FAOstat, 2012) (Figure 3). This map represents the countries where taro was cultivated between 1961 and 2011.

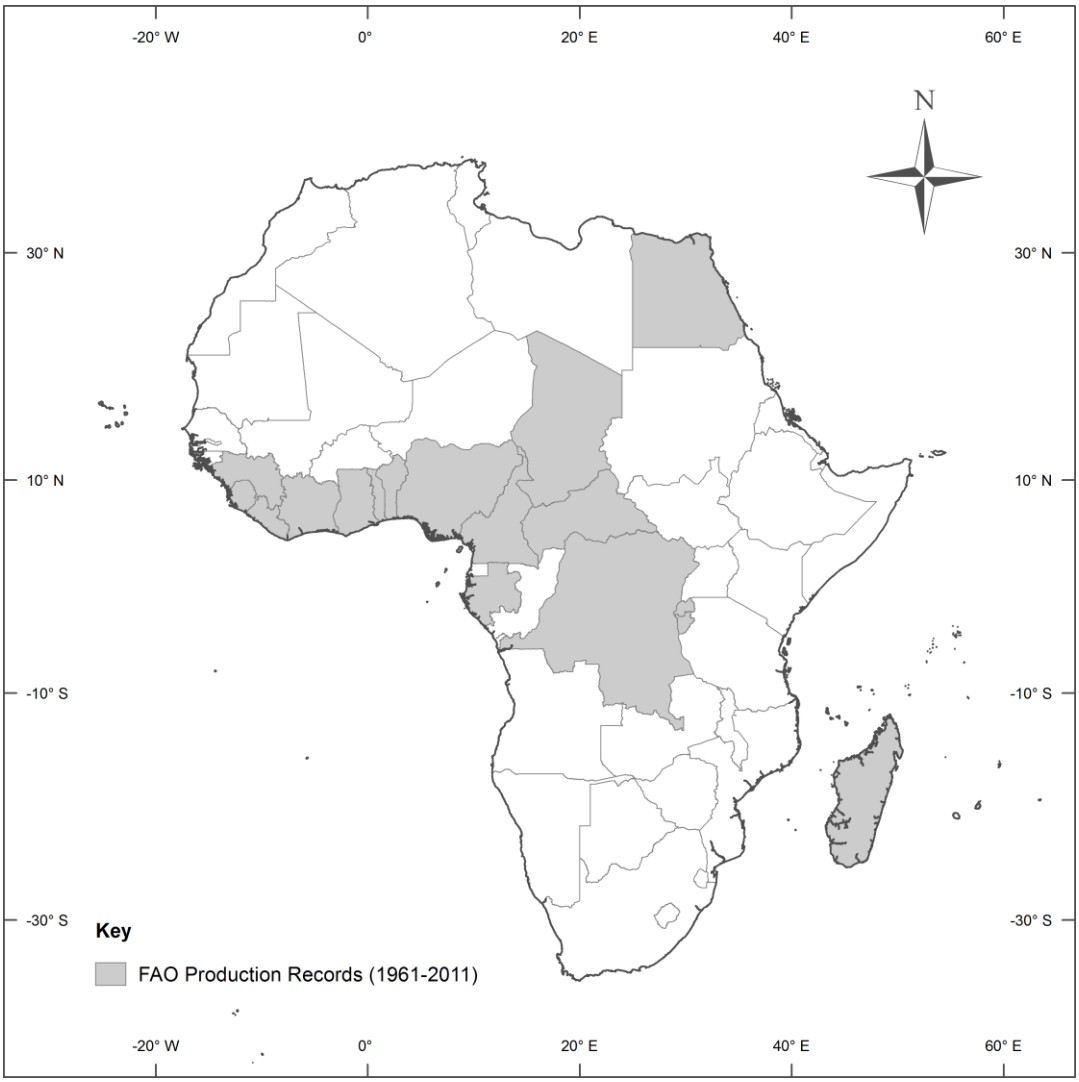


Figure 3. Map of taro production in Africa based on FAO data recorded from 1961 to 2011 (FAOstat, 2012).

These maps show that taro is currently cultivated in hot humid areas with high rainfall, such as the tropical sub-Saharan region, but it can also be found along streams in drier areas such as Algeria, Libya and Egypt. The

comparison between data extrapolated from the FAOstat database and historical records reflects where the production is significant in level, and conversely where taro is used as an emergency crop or was historically present which contributes marginally to the overall crop production of the country.

In West Africa taro is a staple, and the corms and flowers are widely used in local cuisine to make *achu* or *fufu*, which is a typical dish made of mashed corms accompanied by sauces made with meat, fish, and other vegetables. In this area, research on taro has been carried out in dedicated centres for root crops such as the Institute of Agricultural Research for Development (IRAD) in Cameroon, and the National Root Crops Research Institute (NRCRI) in Nigeria. The goal of these organisations, among others, is to disseminate information on the agronomical and nutritional values of taro and dispel the idea that taro is a minor crop.

HISTORICAL INFORMATION ON TARO IN AFRICA

The earliest account of taro in Africa comes from al-Masudi (1864: 31). In the 10th century AD, during a journey along the coasts of East Africa, he described his experiences as follows: "the Zanj eat bananas, which are abundant there and in India, but the base of their nutrition is the dorrah and kalari, which they pull from the earth like a truffle and like the root of horse-

heal. It is widely found in Aden and in the region of Yemen nearby this town; it resembles the Egyptian and Syrian colocasia".

Zanj is the name used by medieval Arabic geographers to refer to Bantu-speaking people living in Southeast Africa, and *kalari* appears to be the Malay name for taro *keladi* (Spier, 1951; Portères, 1960; Devic, 2008), which is also borrowed into Swahili as *kiazi* (Tom Hoogervost, pers. comm.). *Dorra*, which is a type of sorghum, or more generally a collective name for several cereals (Devic, 2008), is a staple crop among the Konso tribes of East Africa (Murdock, 1959:200). The association with horse-heal (elecampane (*Inula helenium* L.)) comes not only from the similarity in the exploitation of the roots, but probably also from the similarly sharp taste of its roots, which were prescribed in antiquity to cure stomach disorders (Pliny, NH 19, 91).

Burkill applied the name keladi to sweet potatoes, and similar words are applied to yam (Portères, 1960), but in the 10th century sweet potato had yet to arrive in Africa, and yam is generally less common than taro in East Africa (Murdock, 1960; Wigboldus, 1994). Therefore it is reasonable to assume that taro was already present in Egypt and Syria where it was known as *colocasia,* and in east Africa and Yemen as *kalari*.

Medieval Islamic authors often referred to taro as a medicinal plant used to cure various diseases. A detailed survey of medieval and Ottoman sources carried out by Lev (2002) in the region of al-Shan (Levant) reveals that taro was being prescribed as early as the 10th century to cure inflammation,

wounds, burns, haemorrhoids and sexual disease, or more generally to treat internal diseases. He listed the geographers al-Muqaddasi (946 – end of 10th century) and al-Dimashqi (1256 – 1327), al-Badri (15th century), the Egyptian writer and mathematician al-Qalqashandi (1355 – 1418), and the Syrian physician Daud al-Antaki (16th century) as all describing taro in their works.

Taro was certainly present in Egypt from ca. 1000 AD onwards. The recent discovery of macro-remains of the plant in the archaeobotanical record of the site of Quseir al-Qadim (Van der Veen and Morales, 2011) attests to its presence during the Islamic phase of occupation, with calibrated radiocarbon dates confirming its earliest presence by 1050-1170 AD (ibid. p. 95; Van der Veen and Hamilton 2011, Appendix 1). However, absence of references to the plant in the Geniza documents suggests that taro was not traded as a commodity through the port (Van der Veen and Morales, 2011: 96).

In the 12th century, al-Maqrizi wrote that taro was planted contemporaneously with sugar cane, and referring to Ali ibn Ridwan (c. 988 – c. 1061 AD), mentioned the presence of taro cultivations in the Nile Delta (Müller-Wodarg, 1957:27, 29 in Van der Veen and Morales, 2011:96). During the same period, al-Bagdadi (1162 – 1231 AD) (Portères, 1960; Van der Veen and Morales, 2011) reported seeing taro in Egypt and described it as a plant having roots which were extremely acrid and with an astringent taste, but that once cooked became suitable for use as food.

When and how the plant reached Egypt has been a matter of much speculation and three main theories have been proposed. The first one implies an introduction of taro into Africa via the Nile, although different time windows have been proposed for this introduction. The earliest date of arrival was put forward by Reinhardt (1911 cited in Rivers, 1926: 273), who advanced the hypothesis that taro moved with Iron Age "Megalithic people" from India to Arabia, Egypt, and the East Mediterranean as early as 500 BC. Then, via the Nile, the plant was suggested to have been transported across the continent into West Africa and along the coasts of East Africa (Plucknett, 1976).

Burkill (1935: 639) thought that taro had arrived in Egypt by the time of Christ and that from there it was dispersed across the Mediterranean. He was also convinced that the plant had been introduced at an early date to East Africa through the island of Zanzibar in Tanzania, and that from there and also from the Mediterranean the plant was dispersed across Africa - although he did not suggest who was responsible for this introduction.

Basing his arguments on linguistic evidence, Watson (1983) proposed an Islamic diffusion of taro from the Near East to West Africa via the Nile. In this regard, the recent retrieval of taro at the Islamic port of Quseir al-Qadim in Egypt marked a firm point in time where taro was part of both Egyptian cuisine and agriculture (Van der Veen and Morales, 2011), and suggests that a connection with West Africa would not have been impossible. However, further linguistic studies in West Africa have dismissed the hypothesis of an

Arab introduction in that area (Williamson, 1993; Blench, 1997), and exactly how and when taro arrived on the Atlantic shores remains unknown.

The second theory is that taro was brought by Indonesian Austronesian seafarers to Madagascar, and the coasts of East Africa. As mentioned earlier, this sea-borne route was proposed by Murdock (1959), who on the basis of linguistic, ethnographic and historical evidence, suggested that during the first century AD, Indonesian people, while navigating along the coasts of India, southern Arabia and East Africa, travelled towards the East African coast where they introduced the so-called Malaysian crops to Africa. Once in Africa, Murdock (1959: 225-227) proposed that these crops were transmitted through the Yam Belt, an existing corridor of agriculturalists who would have been responsible for the diffusion of the Malaysian crops to the opposite side of the continent. From equatorial Africa, the plants could then spread throughout Africa.

Typological comparison of musical instruments found in West Africa with those of Asia adds a cultural element to the discussion, and leads into the third hypothesis. Jones (1971) suggested that Austronesians may have arrived early in Madagascar and travelled around the Cape of Good Hope to reach West African coasts. There they would have been responsible for an early introduction of tropical food crops. Although water yam is suitable for long storage (*Dioscorea alata* L.) (Blench, 2007) as is the case for some varieties of taro (Matthews pers. comm.), which lends them to long voyages, this

model requires the endurance of difficult sailing conditions to reach West Africa.

LINGUISTIC RESEARCH ON TARO AND ITS INTRODUCTION TO AFRICA

An indirect way to trace crop movements is to look at linguistic patterns of crop names and their relationship to geography. However, two key caveats need to be taken into consideration in undertaking such studies, the first being that as people migrate, the names they use may be used for more than one thing, and the second being that while internal phonological developments are by and large regular, linguistic borrowings often get distorted (Wolfgang de Melo, pers. comm.).

Around the Indian Ocean, taro has many names. In Southeast Asia the plant is known, for example, as *kelady*, *tallus*, *tallas*, *tales* or *taloes* (De Candolle, 1883). In Sri Lanka the wild plant is known as *gahala*, and the cultivated one as *kandalla* (ibid.), which are similar to the Southeast Asian names. Affinities between the Sanskrit term for taro *kutchoo* and the Greek term *colocasia* led De Candolle (1883) to propose a direct sea-borne introduction of this plant from India or Sri Lanka into the Arabic world. Of the same opinion was Thiselton–Dyer (1918: 299), who referring to another Sanskrit name for taro, *kala-katchu*, reported Sir Charles Lyall's arguments for which *ch* would be pronounced in West India as *ts* and in Northeast Indian as *s*. Following this semantic path,

and using the translation of *kala* as "black", Portères (1960) put forward the idea that the *black kasia*, or the "edible black root" originally came from the basin of Ganges or the Gulf of Bengal. Today, in Northeast India the name *kala kachu* is still applied to taro (Subhash et al., 2012), highlighting the possibility of a strong connection between this area and the Greek word *κολοκασια*.

However, it appears that the Greek word *kolokasia* from which the word for modern *Colocasia esculenta* originates, was initially applied to the tubers of what botanists have recognized as *Nelumbo nucifera* Gaertn. (Woenig 1897), the sacred lotus plant of India. Neverthless, Thiselton–Dyer (1918: 301) did not see an issue in suggesting this word as a general term for tubers in the Classical world. A review on the use of the Greek word *colocasia* and other names is documented in Chapter 6 "Taro in the Mediterranean world".

TARO PRESENCE IN NORTH AFRICA

Taro is an important crop in Egypt, and is fully integrated into the local cuisine. Tächkolm and Drar (1941: 375-377) have extensively studied the plant in their "Flora of Egypt", and following linguistic and historical hints, concluded that taro arrived into Egypt from Syria. They excluded an introduction via Arabia since the plant does not seem to be of great antiquity there, citing a substantial lack of textual evidence that would single out that region as the place of origin.

Since its arrival in Egypt, taro has gradually spread across other North African countries. In Algeria, Meyer (1881) found an Arabic manuscript dated to the 13th–14th century AD in which taro was listed amongst medicinal plants with the names *louf*, *siaoun* and *kolkace*, or commonly *colocasie* or *colocasse* (Meyer, 1881: 45-49).

In antiquity, as in modern times, the Nile must have been used as a corridor for taro dispersal. This crop has been reported in central and southern Sudan (Durand and Schinz, 1895; Broun and Massey, 1929; Andrews, 1956), but unstable political situations have so far hampered an ethnobotanical study of taro in this region, making more comprehensive ethnobotanical research in this area a useful exercise for the future (Andrews, 1956).

TARO IN WEST AFRICA

In Senegal, taro grows in the Basse Casamance region (Berhaut, 1988), where it is generally cultivated near houses. It only flowers very rarely or not at all. People use the main corm for consumption, while the lateral corms are used for replanting, although the remains of the corms and the leaves are sometimes used for the fattening of pigs. In Senegal, taro is known by different vernacular names (Berhaut, 1988: 67) in languages and dialects of the Niger-Congo language family. They are listed in Table 3:

Table 3. Names for taro in Senegaland associated languages (after Berhaut, 1988: 67).

Language	Term for taro
Badiaranke	*kumpapa*
Balanta	*taèm*
Bambara	*dabéré*
Bassari	*a-néoré, a-néwuré*
Coniagui	*vangõnd, vénkõnd*
Diola	*usub, usup, é gunday, diabère*
Foula	*diabéré, kok*
Malinké	*dabéré*
Peul	*dabira, dabéré*
Socé	*dabéré*
Wolof	*wasu*

In French Guinea, taro was recorded under the name *chou d'Égypte* (Pobéguin, 1906). Several varieties were said to have been cultivated over a long period of time by the indigenous people for their edible corms, but no morphological description is available for them.

From Senegal and moving southeast taro gradually becomes more important. This is evidenced by the many names applied to taro in this region (Burkill, 1988). Ghana is a region which was known during European colonial times as the Gold Coast, and under the Portuguese, and later Dutch, French and British colonial administrations, slaves were captured, traded, and eventually sent to America where they were used as labour for the cultivation of sugar and tobacco (Carney and Rosomoff, 2009). In West Africa taro is known as *kooko,* with indigenous people considering it native to this region (Irvine, 1930:122) attesting to its long use as a crop. Portères (1960) noted that

a plant known as *kafi* and similar to colocasia was recorded by Ibn Batuta in the Kingdom of Mali (Defrémery & Sanguinetti, 1858: 399), highlighting the possibility that taro could have reached this region by the 14th century AD. Linguistic studies in West Africa have dismissed the hypothesis of an Arab introduction in that area (Williamson, 1993; Blench, 1997), and exactly when and how taro arrived on the shores of the Atlantic remains unknown.

In West Africa, taro occurs in most parts of the forest and is well adapted to wetter conditions, making it suitable for cultivation in swamps and near running streams. Irvine (1930) recorded some varieties growing up to six feet in height with leaves of light green and white fleshy corms which are eaten chiefly by older people. The presence of flowers is also said to be uncommon.

In Nigeria, taro is known as *cocoyam*, and is an important source of starch and protein. The corms are the main part used as food. Some cultivars are eaten after been boiled, fried or pounded into *fufu*, with others being used as a soup thickener (Falade and Okafor, 2013).

Nigeria ranks as the most prolific producer of taro not only in Africa but also in the world, with 3.45 billion tonnes produced in 2012 (FAOstat, 2012). In the northern Nigerian provinces, taro used to be grown upon high mounds or ridges, low-lying meadows, in marshes, swamps and near streams (Dudgeon, 1922: 126). In this region, Holland (1922: 756) recorded taro as being grown by the Hausa, who know taro as *gwasa* or *makani* (Alinnor and

Akalezi, 2010). Dalziel (1937: 481) recorded a good many names for the plant, one of which was *woman's yam* (Cross River State), probably referring to the fact that the cultivation and processing of taro was carried out primarily by women. He saw taro cultivations at Kontagora, located in the northwest Niger State in Nigeria, although he noted that it was more commonly grown in the south (Dalziel, 1907: 206). Also, Dalziel noted that the varieties cultivated on the coast and in forest areas were scarcely improved, but that in the interior they were free from acridity and good for food (flood plains and generally wetter environmental conditions must have favoured taro cultivation in the interior), although were in a phase of replacement (1937: 481). Generally speaking, the corms of this crop are used in this region as a food source, although medicinal uses are often recorded. In the southwest region of the country, in the Ondo State, Oka Akoko people know taro as *Koko poso* and squeeze the leaves to extract juice which is used to strengthen premature babies (Obata and Aigbokhan, 2012). The Oka Akoko also believe that taro has magical powers, such that if the leaves are burnt with other material and set into the air, they have the capacity to stop rainfall (Obata and Aigbokhan, 2012).

In Nigeria, linguistic studies have suggested that taro has ancient origins. Williamson (1970) indicated a likely introduction for this crop in the central and western Delta from the northeast, approximately located in the Igboland (the Igboland is a cultural region and linguistic area in Nigeria

defined by the Igbo ethnic group). How the plant arrived there is uncertain. If taro entered into Africa via the Nile, the plant must have been known by a term different from the Arabic name *qolqas*, as it seems that linguistic association is difficult to interpret (Williamson, 1993; Blench, 2004). According to Blench (2004), the adoption of terms for taro from the Chadic languages rather the Arabic *qolqas* constitutes further evidence that does not favour a Nile introduction. In fact, a recent genetic study has linked Chadic-speaking people and Afro-Asiatic populations from North Africa, with a model of expansion dated to the mid-Holocene (Cruciani et al., 2010). This period is too early to indicate an introduction of taro via Egypt, but established connections between North Africa and an area of now non-existent lakes in Central Africa could have represented important geographical corridors for human and plant movement later in time.

Taro is present in Niger (Vogel et al., 1849), Chad (Ramsar, 2005) and also in the Central Africa Republic where it is known as *bombia* by the Banda people, and *toféima* by the Mandja people (Chevalier, 1913: 1020). Here, Chevalier recorded three varieties of taro. Two of these were described as having a purple petiole and purple blade leaf nerves, with the third variety having a green petiole and green blade leaf nerves. It is likely that changes in climate and agricultural practices could have affected the presence and distribution of taro in this area. This makes the ethnobotanical and genetic study of taro growing in this region all the more important.

Taro is also present in Cameroon (Ntèpé-Nyame, 1988) where it is a staple (Murdock, 1960). A survey in this area has highlighted the central role that taro occupies in the local culture, and the results of this survey are treated in Chapter 4 Ethnobotanical observations of taro in Africa.

TARO IN EAST AFRICA

In East Africa, taro does not seem to have the same importance as it does in West Africa. In both regions, changes in the environment and in agricultural systems have led to a general decline in taro production in recent times, and it is now mainly elderly people who remember the older taro cultivars and who are aware of the introduction of new plants.

The most recent ethnobotanical account for taro in Africa is from Fujimoto (2009). He observed taro cultivations in South Ethiopia in highland and lowland areas looked after by forty different ethnic groups. In this country, taro is known as *boyna,* but Fujimoto actually reported 36 names for taro cultivars which were recognized on the basis of their morphology. *H'are boyna* is the name for wetland taro, but this variety is not particularly valued because cultivation in the wetlands leaves it damp and limp. *K'aare boyna* is the name for wild taro, but this variety is very acrid and is used only during times of famine.

The cultivation techniques differ in the highlands and lowlands, and duties are generally shared between men and women. In fact, men are responsible for weeding, and women for harvesting. In the lowlands, taro is grown alongside other crops such as banana and coffee, but in the highlands taro is a monocultivation. Taro is planted from March to May and harvested from September to January and from November to December in the highlands (Fujimoto, 2009), reflecting the effect of temperature in its growth. Taro is cooked by peeling or scratching the skin, with the corms then steamed and boiled along with other vegetables. Compared to the *fufu* of West Africa, taro in Ethiopia is not heavily pounded, but it is roughly mashed to a mealy texture. Leaves and petioles are not generally eaten, but instead are used to wrap things up.

Fujimoto (2009), reporting Safo Kantaka (2004), noted that in Africa taro is represented mostly by the eddoe type, and that this type of taro is more frequent in lowland cultivations, whereas the dasheen type taro is generally cultivated in the highlands. Because lowland environments are drier than highlands, Fujimoto suggested that this could reflect the adaptability of eddoe type to less wet climates.

In Kenya, taro is grown in Nairobi and the Central and former Eastern provinces (Maundu et al., 1999). In this country, one of the first accounts of the presence of taro comes from Hobley (1895), who in 1892, during a journey in the southern part of Kenya, recorded the *mayugwa* of the Kikuyu near the

Bura Valley, which he said was a variety of '*colocassia*'. Hoorweg and Niemeyer (1980) studied the Kikuyu's food habits and listed taro, recorded with the local name *arrow root* and the Kikuyu name *nduma*, as a lesser used root crop. *Ndumaya Mwanake* is said to be the most primitive variety of taro (Maundu et al., 1999). This variety is particularly acrid and irritates the mouth and throat, and has now been substituted with new improved varieties (Maundu et al., 1999).

Currently, taro cultivation is still practised by the Kikuyu people, a Bantu ethnic group who live in the area of Mount Kenya, although the plant is not unique to them. The Meru people, who live on the eastern fertile lands of Mount Kenya, use the name name *ituma* (singular) and *matuma* (plural) for taro, with the leaves known as *maguru* (Maundu et al. 1999). They use both the leaves and the corms of taro in their cuisine. The Tharaka people, who occupy the low plains between Mount Kenya and Tana River, also call taro *ituma* (Maundu et al., 1999). On the coasts, a small tribe known as Chonyi know taro leaves as *maburu*, with the word *nduma* being used for the corms (Maundu et al., 1999). On the other side of Kenya, close to the border with Uganda, the Bukusu, a tribe of the Bantu ethnic group Luhya know taro as *litolotolo* (Maundu et al., 1999).

Usually, taro is cultivated at the bottom of valleys where water collects, or near streams. However, environmental changes and the disappearance of

some streams have caused a reduction in taro cultivation (Were and Wandibba, 1986 in Kimathi, 2011).

In terms of tropical East Africa flora, which includes Uganda, Kenya and Tanzania as a group, Mayo (1985) reported a list of five cultivars of taro, all correlated by names and morphological descriptions. They are listed in Table 4:

Table 4.Varieties of taro listed in Mayo (1985).

Name of the variety	**Morphological description**
Msaru	Petiole light green, veins with flanges of lamina tissue on underside[1]
Mshele	Plant up to 1 m. tall; petiole dark red, leaf-blade dark green
Msaanga	Plant up to 0.75 m. tall; petiole red-striped at base
Msale	Plant up to man height; petiole entirely dark green, blade similar.
Mujasa	Plant very tall; petiole entirely light green, tuber not used for food

Williams (1949), who refers to taro as *Chinese eddoe* and *Mayugwa*, reported three varieties of taro in Zanzibar: two varieties of taro eddoes, and one type of dasheen. The name eddoe was reported by Winterbottom (1803: 64) for plants of yautia (*Xanthosoma sagittifolium* (L.) Schott) introduced to Sierra Leone by African Americans who had migrated from Nova Scotia at the end of the 18th century. However, eddoe has now become the agronomic name for cool-adapted cultivars of taro that have a central mother corm and many corms around it. While Williams reported that the dasheen type is not cultivated, the eddoe types were described as having pale green leaves and

[1] The reader can refer to Figure 29 at pag 113 .

stalks. This is the most common type, the leaves of which are consumed as a green vegetable, together with another variety recently introduced from South Africa, with a dark-green leaf, red petiole junction, and reddish leaf stalk, and better adapted to moist soil conditions. Walsh, describing plants used during periods of famine in Pemba (2009), cites a 1970s account in which taro, among other plants, was used as a green vegetable. According to these earlier accounts, taro was known in Zanzibar as *mayugwa*, and the leaves as *majimbi* with these names also being applied to yautia.

Linguistic connections that link Madagascar with Southeast Asia have long attracted the attention of scholars who usually associate taro arrival in Africa with Austronesian seafarers suggested to have settled on the island during the first millennium AD (Murdock, 1959; Blench 1996; Beaujard, 2011). However, comprehensive ethnobotanical research has not been carried out on taro in Madagascar to test this idea to any degree. On Madagascar, taro is cultivated in the wetter regions, especially on the eastern side of the island, as well as in the Central Highlands (Murdock, 1960). In 1987, Henry Wright of the University of Michigan collected four samples of taro from Madagascar, which were used in this study. Wright noted that the samples collected represented two types of taro, the first one known as *Soanjo Gas*y ("Malagasy Taro") or *Soanjo Mamy* ("Sweet Taro") distinguished by smaller, darker corms. The second type was known as *Ramandidy* or *Ramandady*, with larger, light-coloured corms, believed to be a recent introduction (Henry Wright pers.

comm.). *Saonjo* is the general term used for taro in Madagascar though here are many vernacular names for it, such as *anantsaonjo* and *horirika* (Merina people), *majimbi*, *pakalelona*, *sahonga*, *sahosiloa*, *saonjo*, *saony-saona*, *sohono*, *sonjo*, *taho* (Betsimisaraka people), *tarela* and *taro* (Tanala people). Moreover, some cultivars are known as *sahomamy*, *sahomavo*, *sahombia*, *sahongoaka*, *saonjohary*, *sonjoramandady*, *sonjorika* (Bogner, 1975). The Mikea group of hunter-gatherers who live in the southwest region, are known to collect taro among other tubers (Stiles, 1998). Taro is also embedded in the local folklore (Sibee, 1891; Haring, 2002), is used in rituals and is subject to taboos. For example, bridal couples have to eat taro as a sign of prosperity and fertility, but a pregnant woman cannot cross a field where taro has been planted (Watts, 2007).

Taro is also grown in nearby islands. In Mauritius, taro is known as *arouille* in certain varieties where only the corms are eaten, but in some others the blades are also used as food. In La Réunion, taro is known as *songeosonzedy pays* (de Cordemoy, 1895), but there are many varieties (e.g., *sonze de Chine*, *sonze du Maurice*). The leaves and the corms are used in the local cuisine, but there is a variety known as *sonze noire* (black taro), which is not edible and is found in the wild along streams and watercourses.

TARO IN SOUTH AFRICA

In South Africa taro is known as *amadumbe* in Zulu, *madoembe* in Afrikaans and *madumbe* in English (Nkabinde, 1998), where the Zulu term probably refers to the swollen underground stem word in Zulu, *dumba* (Shange, 2004). Taro cultivations in South Africa are mainly found in coastal regions between Bizana and the KwaZulu-Natal district. Here, taro is a staple and often seen as an indigenous crop, the leaves and corms of which are used exclusively for food consumption and not as fodder or for medicinal uses as seen in other countries (Shange, 2004). Even though the leaves of taro represent a good source of protein (Oliveira and De Carvalho, 1975), their use is nonetheless ascribed to a lower status, with the corms generally considered as the main edible part. Taro is also grown in the Eastern Cape (Hajdu, 2006), Western Cape, and to a lesser extent in Mpumalanga (Coertze and Allenmann, 1996; Jill, 1987; Laugghlin, 1998) and Limpopo provinces (Modi, 2013). Cultivations of taro are generally less frequent in the central regions, and almost absent in the north where temperatures are higher and drier conditions prevail (Shange, 2004). Although taro is cultivated in wetland and dry land conditions in this region, field experiments have shown that the production of taro in wetlands produces a higher yield than in drier conditions (Shange, 2004). The enhanced harvest is attributed to the use of corms with shoots and high plant density that would improve photosynthesis.

On the other hand, pressures on land use, lack of seed and transportation are the main constraints for the cultivation of taro in this area (Shange, 2004).

To date, the lack of genetic research on taro in Africa has limited the improvement of the existing material for farmers and consumers (Mabhaudhi and Modi, 2013), but recent interest in the genetic characterisation of taro plants is now in evidence. In particular, van Rensburg et al. (2011) have looked at the genetic variation of selected taro landraces collected in South Africa and Nigeria. A high level of genetic diversity was observed within the South African collection, and three major clusters have been identified between plants originating from different regions. In particular, the similarity of plants collected in South Africa with those from Nigeria, and in general of plants coming from different collection sites, highlights the assortment of plants in both regions. This information is also supported by ethnographic data collected from farmers, which infer an exchange of taro germplasm between West and South Africa.

Ethnobotanical research conducted on taro in Kwazulu-Natal reported that farmers distinguish between three types of taro. Based on their petiole colour, the three types of taro are referred to as "red type" (described by Joubert and Allemann (1998) as dasheen), "white type" (described by Joubert and Allemann (1998) as eddoe) and the "Zulu type", in which the use of the word Zulu suggests this type is considered to be indigenous (Shange, 2004). The Zulu type is similar to the "red type", but generally smaller in appearance

and with smaller and more corms which can be irritating in humans. Because of its acridity, the Zulu type is not cultivated, and the red type is preferred for its taste, even if this has a drier texture compared to the white type (Shange, 2004). Here, taro is also subject to taboos, with the white type not being cultivated because of the belief that its cultivation would be a bad omen for the head of the family who could die prematurely, although in reality the reason might be more to do with the poor taste of this variety (Shange, 2004).

A recent study of agro-morphological characteristics and microsatellite screening of selected landraces has shown that morphological diversity in South Africa is not necessarily correlated with genetic diversity (Mabhaudhi and Modi, 2013).

TARO ACROSS THE ATLANTIC OCEAN

Given the historical accounts, it is reasonable to suppose that by the end of the 15th century, taro had reached West Africa. There are no specific accounts of taro unfortunately, as the Portuguese used collective names for tuber crops (Carney and Rosomoff, 2009). Taro was part of the African slave diaspora, when millions of native African people were transported to America and used as slaves to produce commodities for re-sale in Europe. During this process, people carried ideas, diseases, and cultural identities in which food represented what Carney and Rosomoff (2009: 66) described as "resilience against adversity".

When the African slave trade commenced, slaveholders, traders and the slaves themselves had to be fed, and thousands of tons of foodstuff must have been produced to feed them. In the sixteenth century, forts were to be seen along Guinea coasts where slaves had been gathered before they were deported across the Atlantic to the Americas. Provisions for journeys that lasted two or three months had to be collected before leaving, and the demand was mostly met by crops grown in Africa. Thus, the human trade brought about the development of markets, which supplied food in great quantities for Europeans, African middlemen and slaves alike. Human trafficking fundamentally changed food production strategies. In America, initiatives were undertaken by the slaves themselves to plant crops for their own consumption, and provisions that were occasionally left over from slave voyages may have been a source of planting materials (Carney and Rosomoff, 2009).

The initial production of sugar in the Mediterranean and Africa, and subsequently in the Americas, also opened up routes for other crops such as coffee, tobacco, cotton and rice. African yam and plantains had a bigger impact on the New World tropical food system (Carney and Rosomoff, 2009), but taro also crossed the Atlantic and became widespread in the New World. The image of ships crowded with slaves and crops stored on board is far from romantic; however, this was how many plants crossed the Atlantic, giving substance – and perhaps hope – to the migrants.

Many of the plants carried across the Atlantic were unknown to Europeans, and consequently were given new and generic names. Sometimes crops were named after their place of departure, as in the names 'guinea squash', 'guinea melon' or 'da costa' or 'da terra', to indicate that they were from the coast or from inland. Taro became known by the common name 'inhame da costa' together with African yams, *Dioscorea* spp. (Carney and Rosomoff, 2009: 103).

There seems to be no specific record for the introduction of taro in the Americas, part of the problem being that yautia and taro are similar in appearance, and often have collective names (Burkill 1938). Richard Ligon (1657) noticed that in Barbados, African people cultivated roots that grew from 'seeds' (i.e. planting stocks) that the slaves had brought with them during the voyages. His description given for this crop is of plants with big leaves, which are eaten along with the roots, and which are suitable for long voyages - suggesting that he was referring to taro (Carney and Rosomoff, 2009). One of the earliest accounts is from Sloane (1707) who recorded taro at Madeira, Jamaica and Carolina. Sloane (1707) noted that African slaves considered taro a blessing and were delighted by this food.

Linnaeus (1753: 481) described two species of taro, the first one as *Arum colocasia*, based on plants collected in the Mediterranean rim, with the second one known as *Arum esculentum* from specimens of taro collected in

Barbados, and it therefore seems reasonable to think that the New World received taro first from West Africa, and later from the Pacific region.

CONCLUSION

Ethnobotanical and historical data on taro in Africa is sparse and generally difficult to find. In this chapter a more comprehensive picture of taro in Africa has been given, with the aim of providing a solid background from which to assess the history, presence, and use of the crop in countries where it is grown. Gaps in knowledge were identified:

- A general lack of recent ethnobotanical research, particularly in geographical areas such as Sudan and Central African Republic.
- Lack of morphological descriptions for taro in West Africa.
- Scarce genetic research on taro in Africa that has limited the improvement of the existing material for farmers and consumers.

CHAPTER 3 MATERIALS AND METHODS

In this chapter, the plant material used in this research and the methods employed to analyse it will be presented. Material collected during fieldwork, as well as specimens gathered from third parties, is shown in Appendix 2 and Appendix 3 at the end of this thesis.

PLANT MATERIAL

FIELDWORK ITINERARY (ROUTES, DATES)

As part of this doctoral research, fieldwork was undertaken in Africa from the 15th January to 7th April 2010 to gather ethnographic data and to collect samples of *Colocasia esculenta* (L.) Schott. The journey included a visit to the Democratic Republic of Congo (DRC), Cameroon, Kenya and Tanzania (Figure 4 for a map of countries surveyed in Africa), with the aim of achieving representative coverage of the current distribution area of this crop.

Due to the limited knowledge of the current *Colocasia esculenta* distribution area, the Bioversity International in Rome was contacted on the advice of Peter Matthews. As a result of this, prior to beginning this research, the author met Mrs Adriana Alercia, germplasm information specialist who supervised and coordinated the production of the *Descriptors for taro* (*Colocasia esculenta*) (IPGRI, 1999) for which she also provided scientific and technical

expertise. The booklet she authored presents guidelines for farmers, breeders, curators and researchers and lists information useful to the characterization and identification of crops in the field as well as in-house collections. Also, the author met with Dr Danny Hunt, who from 2000 to 2003 worked as the Head of the TaroGen Project (Taro Genetic Resources: Conservation and Utilization Project) at the Secretariat of the Pacific Community (SPC) at Suva, Fiji Islands. During the TaroGen Project, Dr Hunt organised an international team of researchers, farmers and local community members for the implementation of a strategy for the collection, characterization, genetic improvement through breeding, and conservation of the germplasm collection of *Colocasia esculenta.*

Mrs Alercia suggested contacting the germplasm banks that contain C*olocasia esculenta* found in The World Information and Early Warning System (WIEWS) database on Plant Genetic Resources for Food and Agriculture (PGRFA), established by the Food and Agriculture Organization of the United Nations (FAO). However, as pointed out in the Edible Aroid Conservation Strategies document (Rao et al., 2010), and as also experienced by the author, the information is mostly out of date.

At the beginning of this research (October 2009), the scientific understanding of *Colocasia esculenta* in Africa comprised a series of publications on the nutritional value (e.g. Ejoh et al., 1996; Lewu et al., 2009), starch composition (e.g. Njintang and Mbofung, 2003a), seed production (Wilson, 1979), and a study describing the cultivar diversity and agriculture

practices in South Ethiopia undertaken by Dr Fujimoto (2009). The lack of information about *Colocasia esculenta* cultivation areas - with the only exception being the area around Lake Victoria (Talwana et al., 2009) - therefore led to the development of a strategy for the acquisition of material to be used in this study.

In order to be able to test the hypotheses put forward by scholars and discussed in the first chapter, it became clear that samples from the African equatorial area were needed.

Burkill, in the "Useful plants of West Tropical Africa" (1938), listed all the common and vernacular names applied to *Colocasia esculenta* in Cameroon, Gambia, Ghana, Guinea, Guinea-Bissau, Ivory Coast, Liberia, Mali, Niger, Nigeria, Senegal, Sierra Leone, Togo and in the West Region of the Republic of Cameroon. However, it quickly became apparent that in these West African countries *Colocasia esculenta* is known under many local names. This picture could erroneously lead one to assume that the high number of words for this crop reflects a corresponding number of varieties, and that a high genetic diversity of the organisms would indicate a long history in that area. In this regard, it has been argued that if the name of a plant has the same root in different languages, it indicates that the word is not part of the core language (Williamson, 1993; Blench, 2009) and therefore it is very likely that the plant was introduced at some point in the past.

However, if we assume that a new crop is introduced in a new environment where there are no competitors, it is possible that the organism shows high morphological diversity but at the same time retains similar genetic features. This picture can be explained by a founder event, in which a few individuals with a narrow genetic signature start a new population. Two founding events are expected to give rise to different phenotypic effects in this respect, hence repeated founder events will give the appearance of cultivar diversity.

To clarify this issue, Nigeria was targeted as a good country to conduct fieldwork, as shown by Burkill (1938) to contain the majority of names listed. However, the original idea of going to Nigeria was replaced by the decision to sample in the Democratic Republic of Congo DRC, where *Colocasia esculenta* is also a staple crop. This choice was due to the fact that during the planning phase of the fieldwork Nigeria developed an unstable political situation due to terrorist attacks in the delta and northern regions. Although the sampling would have not covered those areas, the author was advised by the Italian Foreign Ministry of Affairs to cancel the visit. Nonetheless, samples from Nigeria were kindly provided by Mr Israel Borokini. Mr Borokini collected not only plant material, but also provided linguistics information about *Colocasia esculenta* in Nigeria and information about basic morphological traits that will be discussed where appropriate.

The Cameroonian contact was suggested by Father Martin Nkafu, a local priest, who established contact with his relatives in the South West Region. They have grown *Colocasia* for a long time, and agreed to be field assistants. A meeting with Mr Ephraim Che was then arranged in Douala, who assisted in sample collection for the duration of this part of the field trip.

In terms of the Kenyan collection plan, Mr Daniel Wanjama was located through on-line research. Mr Wanjama is an official of the Kenyan Ministry of Agriculture, and had produced a leaflet on traditional cultivation of *Colocasia esculenta* in the highlands of Kenya. A field trip was planned that commenced in February 2010.

In Tanzania, fieldwork was conducted with Mr Fuad Mohammad who helped to collect samples and gather ethnobotanical information in the area of Zanzibar where feral plants of *Colocasia esculenta* normally grow. The rest of the trip was conducted without local support.

According to the *Flora of Italy* (Pignatti, 1982) *Colocasia esculenta* has been recorded as naturalised in Southern Italy, particularly in Calabria, Sicily, and Sardinia. A short season of fieldwork was therefore conducted in Tropea (Lamezia Terme province (LT), Calabria) and at the botanical garden of Palermo (PA, Sicily).

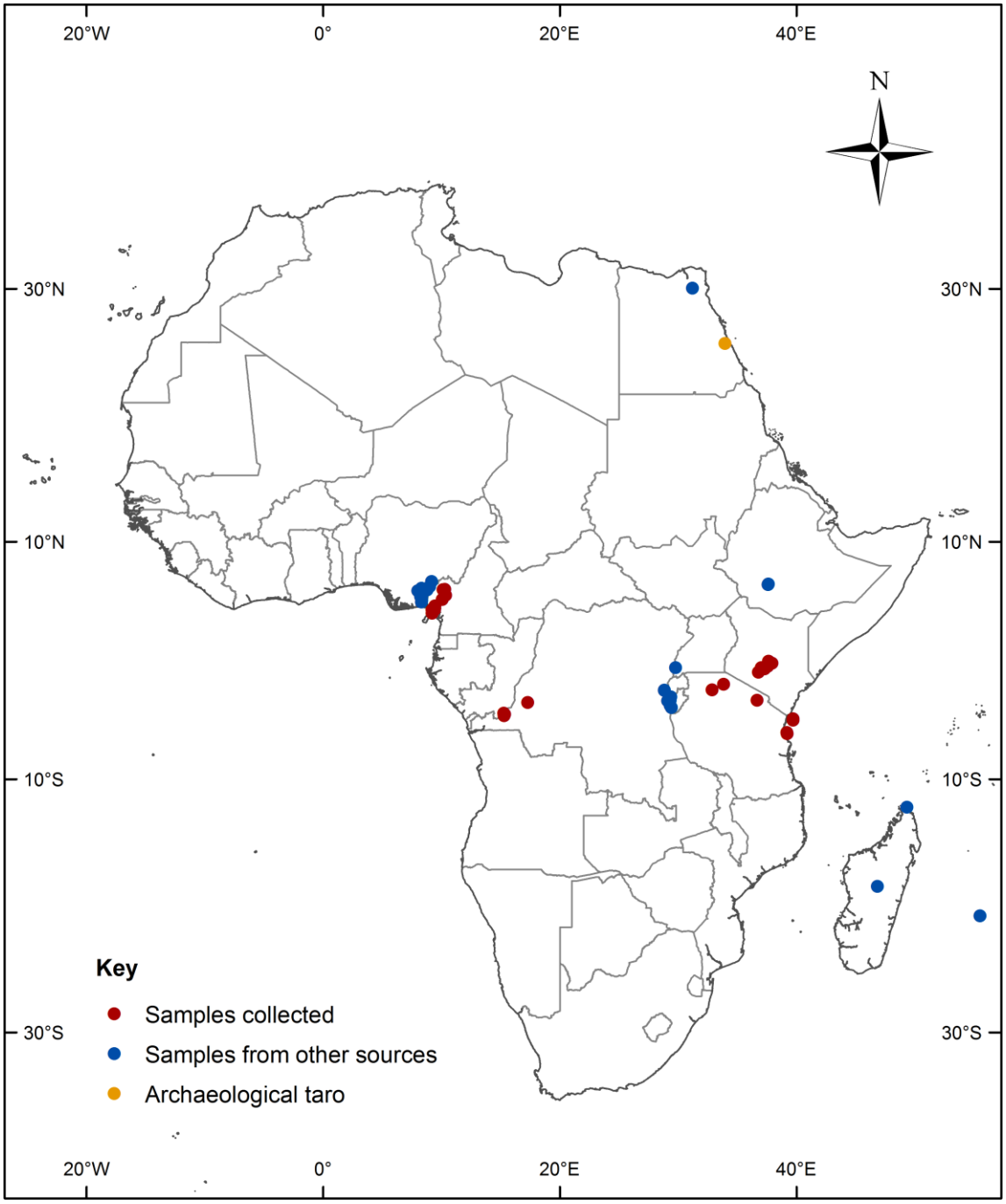


Figure 4. Map of African taro collection (after the U.S. Central Intelligence Agency, 1986). Red dots represent sampling sites covered by the author; blue dots symbols represent sampling sites covered by third parties; the orange dot represents the archaeological site of Quseir al-Qadim from where taro was retrieved.

SAMPLE COLLECTION, TRANSPORT AND STORAGE

A sampling strategy and a sampling protocol were developed for the fieldwork – although due to difficult political situations in some countries, these had to be modified on occasion.

SAMPLING PROTOCOL

After cutting a section between two major veins of the youngest mature leaves, the plant material was then dried between papers overnight and subsequently placed in separate paper envelopes with silica gel. Each envelope was marked with an identification sample code that lists the number of the site of collection and the number of samples at that site. The information was completed with details of the type of environment, satellite coordinates, altitude, morphological features and, where possible, a photograph of the plant.

Dried samples were stored in silica gel during the course of the fieldwork and sent at the conclusion of each country's collection to the School of Archaeology, Research and Laboratory for Archaeology and the History of Art (RLAHA) at the University of Oxford, UK.

OTHER SAMPLE SOURCES

MODERN MATERIAL

In this study, 733 plant specimens of *Colocasia esculenta* were used. A total of 491 leaf samples and two flowers were collected during fieldwork conducted in the Democratic Republic of Congo (DRC), Cameroon, Kenya and Tanzania and in Italy. The remaining 242 samples were provided by other people (refer to Figure 8 pag. 86 for an overview of the countries where samples were collected by third parties and used in this study). The Appendix 3 at the end of this document has a detailed list of samples, including the collector's name, the sample identification number, the country and site of collection, and where possible the geographical information such as satellite coordinates and altitude.

Two of the Malagasy samples were provided by Dr Steven Goodman (The Field Museum of Natural History Chicago, Illinois, USA); the Congolese and the Ugandan samples were supplied by the Nuns of Saint Joseph of Turin (Uvira, DRC); other samples from DRC were collected from Mrs Gerarda Buffa; the Nigerian samples were received from Mr Israel Borokini (National Centre for Genetic Resources and Biotechnology NCGRB, Ibadan, Nigeria); samples from La Réunion were provided from Mr Jacques Eucalyptus (Sud Savage, La Réunion); samples from Burundi were collected from Dr Paolo Monti (FIMAC Onlus (Fondazione Italiana Medici per l'Africa Centrale, Rome,

Italy); the Sri Lankan and Indian samples were collected by Dr Nicole Boivin (University of Oxford, UK) and Dr Dorian Fuller (University College London UCL, UK); Ethiopian samples from Dr Dorian Fuller and provided by Dr Peter Matthews; samples from Assam (India) were provided by Prof Dilip K Medhi (Gauhati University, Assam, India); Dr Peter Matthews (National Museum Ethnology, Kyoto, Japan) provided samples from Madagascar, Egypt, Cyprus, Sri Lanka, India, Nepal, Thailand, Japan, Papua New Guinea, Australia, Solomon Islands, Philippines, Portuguese Timor, Easter Island, Hawaii. Some of these samples belonged to an existing collection of samples from Dr Peter J. Matthews.

ARCHAEOBOTANICAL MATERIAL

Corm fragments of *Colocasia esculenta* were provided by Prof Marijke Van der Veen from the University of Leicester. These fragments were found in Egypt during excavations at the Islamic port of Quseir al-Qadim. The excavations were conducted between 1999 and 2003 by a British team from Southampton University, under the direction of David Peacock and Lucy Blue (Van der Veen, 2011).

Quseir al-Qadim is considered to be the ancient Roman harbour Myos Hormos, inhabited from the early first century AD to the early-mid third century AD and subsequently re-established by Arabs from the twelfth

century onwards (Van der Veen, 2011). The fragments retrieved at the site belong to the Islamic period, with a calibrated radiocarbon date of ca. 1050-1210 AD (Van der Veen and Hamilton, 2011, Appendix 1). It is a unique and important retrieval because it represents the first and only archaeological evidence of taro in Africa and outside the Pacific.

These fragments consist of cut corm fragments of small size (5-40 mm) together with several other skin fragments, suggesting that the corm was used for culinary preparation. It is worth noting that remains of this plant were found in one Islamic period trench only (T13), not being found anywhere else at the site. Figure 5 shows desiccated corms from which DNA was extracted.

Figure 5. Desiccated corms of *Colocasia esculenta* retrieved at Quseir al-Qadim (after Van der Veen and Morales, 2011).

OUTGROUPS

Although the aim of this study does not include a phylogenetic study at a level higher than species rank, the use of outgroups has been considered to investigate the nature of chloroplast types in higher branches of the tree.

Samples belonging to the genus *Colocasia* such as *Colocasia formosana*, *Colocasia gigantea, Colocasia affinis,* and one sample of *Remusatia vivipara* were used. Two samples of *Xanthosoma saggittifolium* in the tribe of Caladieae, and one sample of *Alocasia spp* were also included in this study. These samples were provided by Dr Peter J. Matthews and were used as outgroups.

ANALYTICAL METHODS

MOLECULAR MARKERS

A variety of methods was developed to assess the genetic variation of organisms. The term molecular marker identifies such methods, which in the last 50 years have dramatically improved the resolution to detect variation among organisms.

The very first molecular markers were allozymes, also known as isozymes, which are enzymes that differ in amino acid sequence but catalyse the same chemical reaction (Kumar et al., 2009). To assess their variation, proteins are run on an electrophoretic gel, and are separated according to the differences in amino acid composition. Although these types of marker have

been successfully used in a wide range of organisms (Schlötterer, 2004), due to their inability to assay and quantify genetic variation at DNA level they have been successively substituted by another class of molecular markers that identify variation at DNA level. Historically (Schlötterer, 2004), Restriction Fragment Length Polymorphism, RFLPs (Botstein et al., 1980), was the follow-up system used to study genetic variation, but due to their disadvantages (a relatively large amount of sample to perform the tests is required, and they are extremely laborious, hazardous and time-consuming (Mittal and Dubey, 2009), they were progressively substituted by more practical and more cost-effective markers.

In the 1980s, the development of Polymerase Chain Reaction, PCR (Mullis et al., 1986), revolutionised molecular biology techniques, allowing the implementation of PCR-based markers, like the Amplified Fragment Length Polymorphism, AFLP (Vos et al., 1995), and the Random Amplification of Polymorphic DNA, RAPD (Williams et al., 1990) and Short Sequence Repeats, SSRs, also known as microsatellites (Jones et al., 2001; Kubik et al., 2001), where the amplification of specific genomic regions has overcome the need of cloning or the use of large amounts of DNA. However, the dominant nature of markers like the AFLP and RAPD and the lack of information about the location on the genome do not make them a suitable marker, resulting in the production of anonymous and less predictable results (Allaby, 2007).

USE OF MARKERS TO CHARACTERISE GENETIC DIVERSITY IN COLOCASIA ESCULENTA

Various types of analyses have been used to characterise genetic diversity in accessions of *Colocasia esculenta*. These include: karyotypes (Yen and Wheeler, 1968), isozymes (Lebot and Aradhya, 1991), ribosomal DNA (Matthews, 1990; Matthews and Terauchi, 1994), esterase isozymes (Nguyen et al., 1998), RAPD (Irwin et al., 1998; Matsuda and Nawata, 2002), AFLP (Kreike et al., 2004; Lebot et al., 2004; Caillon et al., 2006) and finally nuclear microsatellites (SSRs) (Mace et al., 2006; Singh et al., 2008; Quero-García et al., 2009).

Isozymes have been used extensively to investigate diversity of plant species (Hamrick et al., 1990) and although they are not particularly polymorphic and can be influenced by the environmental conditions (Kumar et al., 2009), in the study done on *Colocasia* accessions, they showed more genetic diversity in Asia, particularly in Indonesia (Lebot and Aradhya, 1991). This research was subsequently supported by a study performed using RAPDs, in which material from Indonesia showed higher diversity compared to accessions of Pacific provenance. In this research (Irwin et al., 1998), five groups were identified - the largest group including accessions collected in the Pacific (accessions from Hawaii, Papua New Guinea, Western Samoa, Micronesia, Philippines and Polynesia) and some of the Indonesian accessions, a group of triploid accessions (Japan, New Caledonia and Hawaii accessions),

one group of Southeast Asian accessions (Thailand and Indonesia) and two single line groups of accessions collected in Hawaii and Indonesia.

Another study that made use of isozymes was conducted by Nguyen et al. (1998). From the band patterns, the authors concluded that the Nepalese accessions show genetic variability and tend to cluster separately from other groups. However, the common band patterns found in samples collected in the Yunnan area of China seemed to indicate a higher genetic variation and that this geographic area could have played an important role in taro dispersal.

The use of AFLP to establish genetic diversity of *Colocasia esculenta* in Southeast Asia and the Pacific (Kreike et al., 2004; Lebot et al., 2004) confirmed previous results obtained with the use of isozymes (Lebot and Aradhya, 1991), in which Indonesia shows a higher genetic diversity compared to accessions collected in the Pacific. However, as reported in Kreike et al. (2004), these markers were not able to discriminate between diploid and triploid accessions, highlighting the limitations in their use.

The chloroplast genome has also been investigated. In a wider study undertaken on Araceae (Cabrera et al., 2008), the coding regions of *ribulose-bisphosphate carboxylase* gene (*rbcL*) and *maturase K* (*matK*) gene, and non-coding regions *trnK* intron, *trnL* intron and *trnL-trnF* spacer were used to establish genetic relationships among 97 of 105 aroid genera. The most striking result to emerge from the data is that *Colocasia gigantea* (another

species within the *Colocasia* genus) was grouped together with *Remusatia* spp. and *Steudnera* spp. in the Colocasiae clade. In contrast to these findings, however, in a recent study that made use of four chloroplast non-coding regions (*trnL* intron, the *trnL-F* intergenic spacer, the *rpl20-rps-12* intergenic spacer and the *trnK-matK* region) as well as the nuclear *phytochrome C* gene (*phyC*) to investigate the biogeography of the genus *Alocasia* (Nauheimer et al., 2012), *Colocasia gigantea* was placed outside the Colocasiae clade, and surprisingly identified as the closest relative of *Alocasia* spp. Thus, it was proposed that it be removed from the *Colocasia* genus and inserted instead in the *Alocasia*. Some of the issues emerging from this finding relate specifically to the incorporation of nuclear DNA - as proposed by Cabrera et al. (2008) – in that it played a significant role in a new resolution of the phylogenetic relationships within this diverse group.

In this regard, the characterization of microsatellites for *Colocasia esculenta* (Mace and Godwin, 2002; Quero-García et al., 2006; Hu et al., 2009; Lu et al., 2011) provided researchers with more suitable tools to investigate genetic variation at DNA level. In Mace et al. (2006) microsatellites were used in the analysis of genetic variation among accessions of the Pacific germplasm collection gathered in the *TaroGen* project. The microsatellites used proved to be powerful markers, polymorphic and very informative, and were suggested as a tool for the establishment of germplasm collections of other clonally propagated plants.

The same set of microsatellites, together with an agro-morphological characterization, was subsequently used in research conducted on plant specimens of *Colocasia esculenta* in Papua New Guinea (Singh et al., 2008). These microsatellites aimed to establish a core collection for long-term conservation. This is especially important given that *Colocasia esculenta*, as is the case with many other crop plants, suffers from pest-borne diseases, and due to continuous and catastrophic outbreaks of the taro leaf blight (Chan et al., 1998; Guarino, 2010; Bandyopadhyay et al., 2011; Nelson et al., 2011; Omane et al., 2012), the genetic diversity has been seriously affected in countries where *Colocasia* is a staple.

In light of the different methodologies applied to study the genetic variation of members of the Araceae family, particularly *Colocasia esculenta*, and the results obtained (Quero-García et al., 2009), it was decided that the best method to adopt for this investigation was to use the high polymorphism carried by the microsatellites.

In the next section features of this molecular marker will be outlined and the microsatellites selected for this study will be presented.

Microsatellites

As introduced in the previous section, Simple Sequence Repeats (SSR), also known as microsatellites or Short Tandem Repeats (STR), are repetitive units of 1-6 nucleotides of non-coding regions that are found in the genome (Schlötterer, 2000; Ellegren, 2004). Nevertheless, there is no general consensus on the exact number of repeat units (Chambers and MacAvoy, 2000), so that some authors only consider microsatellites where the repeat unit is up to six nucleotides long (Hancock, 1999), whereas others accept microsatellites whose fragments have repeat units composed from 1 to 8 nucleotides long (Mittal and Dubey, 2009) or 2 to 8 nucleotides (Armour et al., 1999). When the repeat unit increases dramatically in number - usually from 10 to 100 nucleotides - these are usually referred to as minisatellites (Richard and Pâques, 2000), and because of their extreme high level of variation, they have found wide application in DNA fingerprinting techniques (Schlötterer, 2004).

Microsatellites can be informally grouped in simple or composite form according to the composition of the repeat unit, such that simple microsatellites contain only one kind of repeat sequence (e.g. (TA)n), whereas the composite ones contain more than one type of repeats (e.g. (TA)n(GA)n). A more formal way to classify microsatellites is to discriminate between perfect, imperfect, interrupted and composite types (Oliveira et al., 2006),

where in a perfect microsatellite the repeat sequence is not interrupted by any base that do not belong to the original motif (e.g. TATATATA), whereas in an imperfect microsatellite there is a pair of bases between the repeated motifs that does not match the motif sequence (e.g. TATATATA**C**TATATA). In an interrupted microsatellite there is a small sequence within the repeated sequence that does not match the motif sequence (e.g. TATATA**CGTG**TATATATATA) while in a composite microsatellite the sequence contains two adjacent distinctive sequence-repeats (e.g. *TATATATATA***GTGTGTGTGT**) (Oliveira et al., 2006).

The mechanism of evolution underlying microsatellites is still under debate (Bhargava and Fuentes, 2010). The predominant theory suggests that the mutations are due to the slippage of the DNA polymerase that would add or remove one or more units during DNA replication (Hancock, 1999) as well as during PCR amplification (Ellegren, 2004); however, further evidence has suggested that the mutation can occur during recombination either by unequal crossing over in which long microsatellites sequences, more likely, would misalign and produce a longer and a smaller segments (Eisen, 1999), or by gene inversion (Hancock, 1999).

Although compared to other loci present in the genome, microsatellites have a high rate of mutation, there is no uniform mutation rate changing from loci, and species (Bhargava and Fuentes, 2010), having mutation rates in the order of 10^{-2} per locus per generation in *in vivo* replication of *Escherichia coli*,

10^{-3} in humans and of 10^{-4} to 10^{-5} in yeast (Hancock, 1999). Due to this high mutation rate, microsatellites prove to be very polymorphic which makes them useful as genetic markers (Chistiakov et al., 2006).

In the estimation of the genetic distance between two groups of individuals using allele frequency, two different mutation models have been proposed for microsatellites (Deka et al., 1991): the Stepwise Mutation Model (SMM) in which a mutation in the microsatellite unit is achieved by the addition or deletion of one repeat unit, and the Infinite Allele Model (IAM) where each mutation can produce a new allele (Kimura and Crow, 1964). The SMM model was originally proposed by Ohta and Kimura (1973) to model the change in charge of proteins detected electrophoretically, and later applied to microsatellites by Goldstein et al. (1995).

Microsatellites have been found in all organisms (Hancock, 1999). They are abundant (every 30-40 kb DNA), and evenly distributed on all chromosomes (Toth et al., 2000), on all segments of chromosomes and in introns (Ellegren, 2004), and their codominant nature allows the detection of all the alleles present at one locus as they are visible as bands on the electropherogram. Moreover, the relatively short length of these fragments makes them easy to detect and reproduce in a PCR reaction, which is an important feature when handling large sets of samples in population genetics studies.

Until recently, microsatellites were thought to be neutral, in other words, no selective pressure was involved in shaping allele frequency observed at the loci (Schlötterer and Wiehe, 1999). However, Moxon and Wills (1999) showed that the extension of repeats can cause diseases such as Huntington's disease, where the increase in the length of a CAG motif repeat that is present in the *huntingtin* protein gene on human chromosome 4, provokes the production of an altered form of the protein, which causes pathological changes and subsequent disease symptoms.

However, microsatellites also present some methodological disadvantages, such as the previous genetic information which is needed for their characterization in a species and the costs and labour associated with their discovery (Selkoe and Toonen, 2006). However, as discussed earlier in this chapter, microsatellites for *Colocasia esculenta* had been already characterized.

NUCLEAR REGIONS

In order to study the genetic variation of *Colocasia esculenta* in Africa, and allow a comparison with different geographical sets of plant specimens, a selection of microsatellites was also chosen from the study conducted on Asian/Pacific samples (Mace et al., 2006; Singh et al., 2008).

In particular, 12 loci from Mace and Godwin (2002) and two from Hu et al. (2009) were chosen. The selection was based on the quality of electrophoretic pattern, number of alleles and polymorphism. Table 5 summarises the loci selected for this study.

Table 5. Microsatellites selected for this study.

SSR locus	Repeat motif	Primer sequence 5′-3′	Source
Xuqtem55	$(CAC)_5$	F: CTTTTGTGACATTTGTGGAGC	Mace and Godwin, 2002
		R: CAATAATGGTGGTGGAAGTGG	
Xuqtem84	$(CT)_{18}$	F: AGGACAAAATAGCATCAGCAC	Mace and Godwin, 2002
		R: CCCATTGGAGAGATAGAGAGAC	
Xuqtem88	$(CAT)_9$	F: CACACATACCCACATACACG	Mace and Godwin, 2002
		R: CCAGGCTCTAATGATGATGATG	
Xuqtem91	$(TG)_6(GA)_4$	F: GTCCAGTGTAGAGAAAAACCAG	Mace and Godwin, 2002
		R: CACAACCAAACATACGGAAAC	
Xuqtem110	$(TGA)_6(TGGA)_4$	F: AGCCACGACACTCAACTATC	Mace and Godwin, 2002
		R: GCCCAGTATATCTTGCATCTCC	
Xuqtem132	$(TTTGAA)_4$	F: ACCCCGAAAAAGCCAATG	Mace and Godwin, 2002
		R: CTATCACTTGTTCCTCCTTCTC	
Xuqtem223	$(CTT)_9$	F: GAGATGGTGTGAGTAAAGGAAG	Mace and Godwin, 2002
		R: TGGACTACTACTGAAGCAGAG	
Xuqtem228	$(GAA)_5$	F: CCAGACTTCTCTCTACACCAAG	Mace and Godwin, 2002
		R: GATCTGTTGAAGAGATCCGTTG	
Xuqtem247	$(CT)_{10}$	F: ATATTGCCGTCCACTCCTG	Mace and Godwin, 2002
		R: AAAGACTCTCTCCCCAGATTAC	
Xuqtem249	$(AG)_{10}$	F: GACGGTCCAAATGTTAG	Mace and Godwin, 2002
		R: CCAAGGAAGATATTACCAAG	
HK7	$(CT)_{14}TTCTT(CT)_4$	F: GTTGTCCGCCTGTGCGTTCT	Hu et al., 2009
		R: CTCTTGGGAATTCTCCGGGTG	
HK31	$(GT)_6(GA)_{11}$	F: GACGGTCCAAATGTTAG	Hu et al., 2009
		R: CCAAGGAAGATATTACCAAG	

Note: F, forward; R, reverse.

CHLOROPLAST REGIONS

Plants

The small, relatively constant size and conservative evolution of chloroplast DNA makes it an ideal molecule for tracing evolutionary patterns,

especially at higher taxonomic levels. The maternal inheritance has to be taken into consideration when phylogenetics is inferred, however, specific regions within this molecule can be used as DNA barcode markers to identify taxa at the species level.

At the beginning of this research, the chloroplast genomic regions available on the NCBI database were determined by the *rbcL* gene. However, it was not included in this study, as the ability of *rbcL* to resolve phylogenetic relationships below the family level is often poor (Doebley et al., 1990; Bousquet et al., 1992).

Conversely, as discussed in the previous section, the *trnL intron* was used in a study conducted on species belonging to the Araceae family (Cabrera et al., 2008) and only recently investigated on *Colocasia esculenta* (Nauheimer et al., 2012). Since this proved to be a highly variable non-coding region in the chloroplast genome, it was also included in this study.

TrnL intron

Universal primers produced by Taberlet et al. (1991) were tested on the modern material of *Colocasia esculenta*. These highly conserved primers were designed around a more variable region to detect polymorphisms within the chloroplast DNA. In detail, this region can be considered as the intergenic spacer between the *trnT* and *trnL* amplified with primers *a* and *b*, the *trnL* intron amplified with primers *c* and *d* and the intergenic spacer between the

trnL 3′ exon and *trnF* using primers *e* and *f* (Figure 6). A smaller fragment within the *trnL* intron was amplified with primers *g* and *h* (Taberlet et al., 2007) and tested on the archaeological fragment retrieved at Quseir al-Qadim (van der Veen and Morales, 2011).

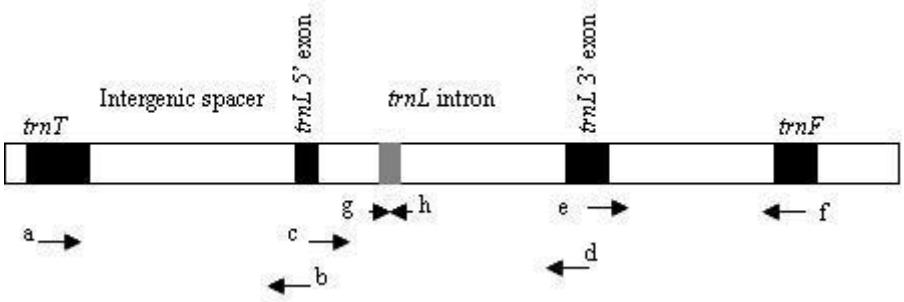


Figure 6. Schematic representation of the cpDNA region between *trnT* and *trnF* (after Taberlet et al., 1991; 2007).

matK and the TrnK intron

The *maturase K* gene (*matk*) is a segment of ca. 1500 base pairs nested within a group II intron (*trnK* intron) in the chloroplast gene that encodes for transfer RNA lysine1 (anticodon UUU) (TRNK1) (Kelchner, 2002) (Figure 7). The protein encoded by the *matK* gene was thought to be involved in the intron splicing activity (Hilu and Liang, 1997), and although mobility seems to have been lost (Hausner et al., 2006), its conserved domain provides a molecule for inferring phylogenetic relationship at various taxonomic levels (Hilu and Liang, 1997).

In this study, 314 base pairs segment of the *trnK* 3′ intron were chosen to infer phylogenetic relationships at interpopulation level. In the ancient fragment of taro, due to the fragmentation of DNA material, this region was divided in two segments, and consequently another pair of internal primers was designed to screen the whole locus that was investigated in the modern material. The two segments - *trnK* intron 1 and *trnK* intron 2 - were subsequently joined together and aligned with the modern samples. Table 6 summaries the chloroplast loci that were investigated.

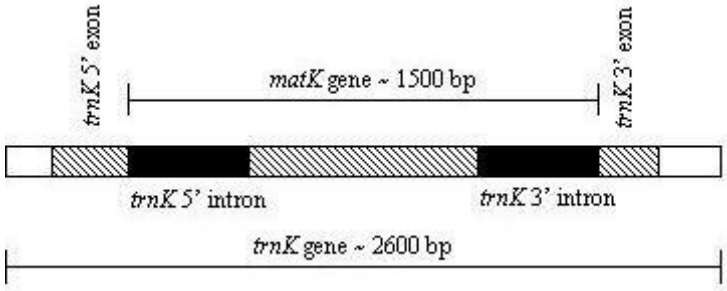


Figure 7. Schematic representation of the *trn*K gene (after Hilu and Liang, 1997).

Table 6. Chloroplast primers sequences, annealing T and source.

cDNA locus	**Primer sequence 5′-3′**	**Annealing T °C**	**Source**
trnK intron (314 bp)	F: CTTTACGGAAGAAGAAAAAGTGC	57	designed
	R: CACGACTTTCCCTATGTATAC		designed
trnK intron 1 (151 bp)	F: CTTTACGGAAGAAGAAAAAGTGC	57	designed
	R: CATGGTCTTATGACTAATGAATC		designed
trnK intron 2 (186 bp)	F: GATTCATTAGTCATAAGACCATG	57	designed
	R: CACGACTTTCCCTATGTATAC		designed
Tab a	F: CATTACAAATGCGATGCTCT	60	Taberlet et al.,1991
Tab b	R: TCTACCGATTTCGCCATATC		Taberlet et al., 1991
Tab e	F: GGTTCAAGTCCCTCTATCCC	54	Taberlet et al., 1991
Tab f	R: ATTTGAACTGGTGACACGAG		Taberlet et al., 1991
Tab c	F: CGAAATCGGTAGACGCTACG	58	Taberlet et al.,1991
Tab d	R: GGGGATAGAGGGACTTGAAC		Taberlet et al.,1991
Tab g	F: GGGCAATCCTGAGCCAA	58	Taberlet et al., 2007
Tab h	R: CCATTGAGTCTCTGCACCTATC		Taberlet et al., 2007

LABORATORY PROTOCOLS

DNA EXTRACTION

Modern DNA extraction protocol

Total genomic DNA was extracted from silica gel dried leaf samples using a modified CTAB extraction method (Doyle and Doyle, 1987). Approximately 10 mg of dried material was ground with a mortar and pestle, and incubated in 1 ml of warm CTAB buffer (2 %) cetyltrimethylammoniumbromide [CTAB], 0.1 M Tris-HCl (pH 8.0), 20 mM ethylenediaminetetraacetic acid [EDTA], 1.4 M sodium chloride NaCl, 1% polyvinylpyrrolidone [PVP]. The contents of the tubes were mixed using a vortex and left in water bath at 65 ºC for two hours or at 50 ºC overnight. The DNA was purified by chloroform:isoamyl alcohol (24:1) extraction, and further purified using a DNeasy® silica column (Qiagen). Double stranded DNA was quantified using Qubit® DNA BR Fluorometer (Invitrogen) following the manufacturer's protocol.

Ancient DNA extraction

DNA extraction was carried out in a dedicated, chambered, ancient DNA extraction laboratory at the University of Warwick Wellesborne campus, using suitable precautions to avoid the intrusion of foreign contaminants. This laboratory had not been previously used to extract DNA from modern taro samples and was located in areas where PCR is not carried out.

Extraction blanks were carried out in parallel with each sample extraction to ensure authenticity. DNA was extracted from two desiccated fragments, ground in a mortar with pestle, and incubated in 1 ml of warm CTAB buffer (2% cetyltrimethylammoniumbromide [CTAB], 0.1 M trishydroxymethylaminomethane [Tris-HCl] pH 8.0, 20 mM ethylenediaminetetraacetic acid [EDTA], 1.4 M sodium chloride) mixed by agitation for 72 hours at 37ºC.

The DNA was purified by chloroform:isoamyl alcohol (24:1) extraction, and further purified using a DNeasy® silica column (Qiagen, Crawley, West Sussex, UK) following the manufacturer's protocol. Double stranded DNA was quantified using a Qubit® DNA HS Fluorometer (Invitrogen) which is designed for material that yields small amounts of DNA.

POLYMERASE CHAIN REACTION, PCR

Inhibitors

Aroids contain needle-shape crystalline inclusions known as calcium oxalate crystals. They are present in the corms, leaves and rhizomes, and are thought to act as defence against herbivores (Sunell and Healy, 1979). Due to their abundance, characteristic shape and ease of detection, these crystals are often used as diagnostic traits for plant taxa (Prychild and Rudall, 1999), which is particularly useful in archaeological research (Crowther, 2009).

However, these crystals, like other phytochemicals (Syamkumar et al., 2003; Dhanya et al., 2007), can function as inhibitors in the PCR reaction. The extracted genomic DNA was therefore measured with Qubit® DNA BR Fluorometer (Invitrogen), and subsequently diluted 10, 100 and 1000 times. Each dilution was tested performing a PCR, with 1000 times dilution producing the best results with a DNA concentration of 1-5 ng/ul. Each diluted DNA sample was then put in a 96 plate and then used to perform PCR reaction for each locus.

MODERN PCR AMPLIFICATION

DNA amplifications were carried out in a total volume of 20ul under the following conditions: 10ng of template, 1 X Buffer 20 mM Tris-HCl (pH 8.4), 50 mM KCl (Invitrogen), 0.65uM of each primer, 0.2 mM of each dNTP, 2.5 mM MgCl2, and 1 U Platinum® Taq DNA polymerase (Invitrogen). Applied Biosystems thermal cyclers were used and thermocycling conditions were extracted from Mace and Godwin (2002), and adapted as follows: 94°C for 5 min, followed by 35 cycles of 94°C for 30s, optimal annealing T° for 30s, 72°C for 30s and a single extension at 72°C for 5 min. To find the optimal annealing T°, TaKaRa PCR Thermal Cycler was used to test PCR reactions to perform gradient PCRs.

Blanks and amplification products were confirmed by gel electrophoresis in 1% agarose stained with GelRed™ prepared according to the following protocol:

1% agarose gel was mixed in 1x TBE (1M Tris pH 8, boric acid and o.5M EDTA). 120ml agarose gel was then aliquoted, and 2.5ul of GelRed™ were added into 1000ml glass flask and mixed in a microwave for three minutes at medium power. The agarose mixture was allowed to cool slightly, while a 96 wells gel casting boat was prepared. The cooled gel was poured into the casting boat and allowed to set for 20 minutes. The combs were removed and the gel was placed in an electrophoresis tank and covered with 1x TBE. 5ul of amplified DNA from each sample was mixed with 5ul colour marker Orange G. A 100bp DNA ladder (Invitrogen) was also loaded in a well at the beginning of each row to verify the authenticity of the products. The tank was connected to the power supply (Lorderan EPS-100) and run for approximately 20 minutes at 100V.

PURIFICATION

QIAvac 96 Vacuum Manifolds PCR purification kit (Qiagen) was used to purify the PCR products according to the manufacturer's protocol. The manufacturer provided the following information regarding the provided constituents of the kit: binding buffer (PM) contained guanidine

hydrochloride and isopropanol. Wash buffer (PE) contained Tris-HCl. Dilution buffer (EB) contained Tris-HCl.

LABELLED PRIMER TESTING

Selected primers of microsatellite regions chosen in Mace and Godwin (2002) and Hu et al. (2011) were labelled with a fluorescent label. Table 7 shows the primers and the fluorochrome associated with them.

Table 7. Primers labelled with fluorochromes and companies that provided the service.

Labelled Primers	Company
NED Xuqtem132	Life Technologies (Applied Biosystem)
FAM Xuqtem88	Invitrogen
VIC Xuqtem228	Life Technologies (Applied Biosystem)
PET Xuqtem110	Life Technologies (Applied Biosystem)
VIC Xuqtem84	Life Technologies (Applied Biosystem)
NED Xuqtem91	Life Technologies (Applied Biosystem)
FAM Xuqtem223	Invitrogen
PET HK31	Life Technologies (Applied Biosystem)

ANCIENT PCR AMPLIFICATION AND PURIFICATION

As in the modern PCR amplification, due to the presence of oxalate crystals in the corm fragment, genomic DNA was diluted 10, 100 and 1000 times, with 1000 times dilution again providing the best results. DNA amplifications were carried out in a total volume of 20ul under the following conditions: 10 ng of template, 1 X Buffer 20 mM Tris-HCl (pH 8.4), 50 mM KCl (Invitrogen), 0.65 uM of each primer, 0.2 mM of each dNTP, 2.5 mM MgCl2, and 1 U Platinum® Taq DNA polymerase (Invitrogen). PCR and extraction blank reactions were carried out in parallel to the sample PCRs. Applied

Biosystems thermal cyclers were used and thermocycling conditions were as follows: 94˚C for 5 min, followed by 10 cycles of 94° for 30s, optimal annealing T° for 30s, 72° for 30s and subsequent 50 cycles of 94˚C for 20s, optimal annealing T˚ for 30s, 72˚C for 20s and a single extension at 72˚C for 2 min. Blanks and amplification products were confirmed by gel electrophoresis in 2% agarose stained with GelRed™. The protocol used was similar to the one used with modern material, the only difference was not only the percentage but also that a small gel casting boat was used, instead of the 96 wells casting gel. Individual QIAquickH (Qiagen) columns were used to purify the PCR products.

SEQUENCING

SEQUENCING OF THE PARTIAL MATK LOCUS IN MODERN AND ANCIENT MATERIAL

Sequencing of 314 base pairs of a *trnK* intron region within the *matk* gene was completed in both directions using 693 modern samples, and one desiccated fragment of *Colocasia esculenta* tuber that was found in the archaeological site of Quseir al-Qadim in Egypt. Following the recommendations provided by the Genomics Laboratory at the Wellesbourne campus of the University of Warwick, the total amplified genomic DNA was first measured with Nanodrop® to calculate the right amount of PCR product to use in the sequencing reaction, then a master mix for the sequencing reaction was prepared according to the Genomics Laboratory's recommendations.

Sequencing was performed using Big Dye terminator v3.1 Cycle Sequencing kit (Applied Biosystems, Foster City, CA, USA) on the following cycle: a first step at 94°C for 1 minute, followed by 25 cycles of 94°C for 10 seconds, 50°C for 5 seconds and 60°C for 4 minutes. The products were eventually separated on a 3130xl Genetic Analyzer.

SEQUENCING OF THE SSR XUQTEM91

Sequencing of 264 base pairs of Xuqtem91 microsatellite locus was conducted on 325 samples, which on the initial genotyped screening were shown to be homozygous.

Xuqtem110, Xuqtem228, Xuqtem132 and Xuqtem223 microsatellites were also amplified and sequenced in the ancient fragment.

SEQUENCE EDITING AND ALIGNMENT

For each sample, electrochromatograms of the forward and reverse sequences were initially visualized with 4Peaks 1.7 (Griekspoor and Groothuis 2005), manually edited and assembled to form a contig with CodonCode Aligner software (CodonCode Corporation, Dedham, MA, USA) and finally aligned with MEGA 5 (Tamura et al., 2011) using the embedded Muscle algorithm. Alignments included the outgroup species: *Remusatia vivipara*, *Colocasia gigantea*, *Colocasia affinis, Alocasia spp.*, and *Xanthosoma sagittifolium*.

STATISTICAL AND GRAPHICAL METHODS

The data obtained from the scoring of genotyping electrophoretic samples were used to calculate values of genetic variability, deviations from Hardy-Weinberg equilibrium, the genetic variability within groups and among groups and the structuring of groups. In this study the term group replaces the term population. Groups were defined geographically; in some cases country's political boundaries were followed, other times, for practical reasons, two or more countries were combined to form one group. For the purpose of this study, 12 groups were identified – Table 8 lists the groups and the number of samples associated with them.

The following programs were used: GENEPOP 3.4 (Raymond and Rousset, 1995), GENECLASS2 (Piry et al., 2004) GenAlEx (Peakall and Smouse, 2012), POWERMARKER (Liu and Muse, 2005) STRUCTURE (Pritchard et al., 2000). PAST (Hammer et al., 2001).

Table 8. Groups defined in this study.

Group ID	Countries	Number of samples per group
West Congo	West part of DRC	39
Cameroon	Cameroon	200
Nigeria	Nigeria	50
Central Africa	South Kivu (DRC), Burundi, Uganda	82
Kenya	Kenya	114
Tanzania	Tanzania	126
Mediterranean	Italy, Egypt, Cyprus	5
Ethiopia	Ethiopia	7
Madagascar	Madagascar, La Réunion	11
India	India, Sri Lanka	32
Japan	Japan	13
Pacific	Australia, Papua New Guinea, Thailand, Japan, Solomon Islands, Philippines, Portuguese Timor, Easter Island, Hawaii	35

GENETIC DIVERSITY

WITHIN GROUPS

In order to measure the intrapopulation genetic diversity, indices that measure the amount of genetic variation were calculated using POWERMARKER (Liu and Muse, 2005). In particular, the polymorphism of a locus measured as $P = q \leq 0.95$ where q is the most common allele frequency (Ott, 1992); the percentage of polymorphic loci, which is simply the ratio of polymorphic loci number divided by number of total loci. The average number of alleles per locus, effective number of alleles and size ranges of alleles were calculated for all samples and for each group of samples. Observed (Ho) and expected (He) heterozygosity were also calculated for each locus and in each group. Moreover, genotype numbers (including numbers of unique and shared haplotypes) were calculated for each sample.

AMOVA

In order to measure the distribution of genetic variation among populations, Analysis of MOlecular VAriance (AMOVA) was also performed. Instead of using alleles' frequencies as in the F statistics, the AMOVA operates directly on molecular data and assesses the genetic differentiation taking into account the mutational differences. AMOVA was assessed with GenAlEx (Peakall and Smouse, 2012). Similarly to the F statistics, this type of analysis is

used to verify how much of the total variance of calculated alleles' frequencies is due to differences found between populations and amongst individuals with groups. Conceptually, it is based on the ANalysis Of VAriance ANOVA, although it does not require a normal distribution. The result is given by the percentage of variance within and among groups, which in this case are the populations, and a *p* value that expresses the probability for two or more groups that the null hypothesis is true. In this case, the null hypothesis is that the groups analysed are identical, or, in other words, that they originate from the same source.

CLUSTER ANALYSIS

Cluster analysis is a hierarchical process of grouping objects in categories or classes based on their common attributes or relationships. A previous study conducted on accessions of *Colocasia esculenta* in Papua New Guinea made use of the Jaccard similarity coefficient (1908) to calculate similarities among pairs of individuals (Mace et al., 2006). When i and j individuals are compared on the basis of their similarities, Jaccard's coefficient is defined as J = a/ (a+b+c), where *a* is the number of times a particular allele is present in both individuals *i* and *j*, *b* is the number of times an allele is present in the individual *i* but absent in *j*, and *c* is the number of times an allele is present in the individual *j* but absent in *i*.

PRINCIPAL COORDINATES ANALYSIS

Ordination methods are complementary to cluster analysis, which summarises the relationships between different individuals by reducing the number of variables that contain all the information about the relationships between groups of objects. One type of ordination method is the Principal Coordinates analysis (PCoA), which can be used to visualize the relationships between genotypes. This method produces measurements of dissimilarities visualized as distances apart and reduces the number of variables, so that all the information can be synthesized in a small number of coordinates. The values -eigenvalues and eigenvectors - are calculated from a genetic distance matrix constructed using the Gower distance (Gower, 1966). To perform the PCoA, PAST (Hammer et al., 2001) was adopted. In the Landmark 3D plot section of this software, a three-dimensional plot can be drawn and animation function allows the visualisation of the groups obtained from the calculation. In this analysis it is assumed that all variables are independent, and the result obtained represents a distribution of the alleles analysed.

BAYESIAN ANALYSIS

STRUCTURE

A Bayesian approach was used to analyse the structure of the populations of *Colocasia esculenta* in Africa. In the use of this software categories are not predefined and are constructed from the given allele

frequencies. On this basis, then, the algorithm assigns each individual in probabilistic way, and the result obtained is the posterior probability that an individual x belongs to a group Y given the estimated frequencies. The software STRUCTURE (Pritchard et al., 2000) was used for this analysis.

ASSIGNMENT TEST

GENECLASS2

Gene flow between populations was examined through GENECLASS2 (Piry et al., 2004). Unlike STRUCTURE, individuals are assigned to pre-defined categories and subsequently are given likelihood to be in the assigned group. First generation migrants are detected and an easy method to analyse gene flow, arrows can be designed on a map from the designated source population to the populations from which they were collected.

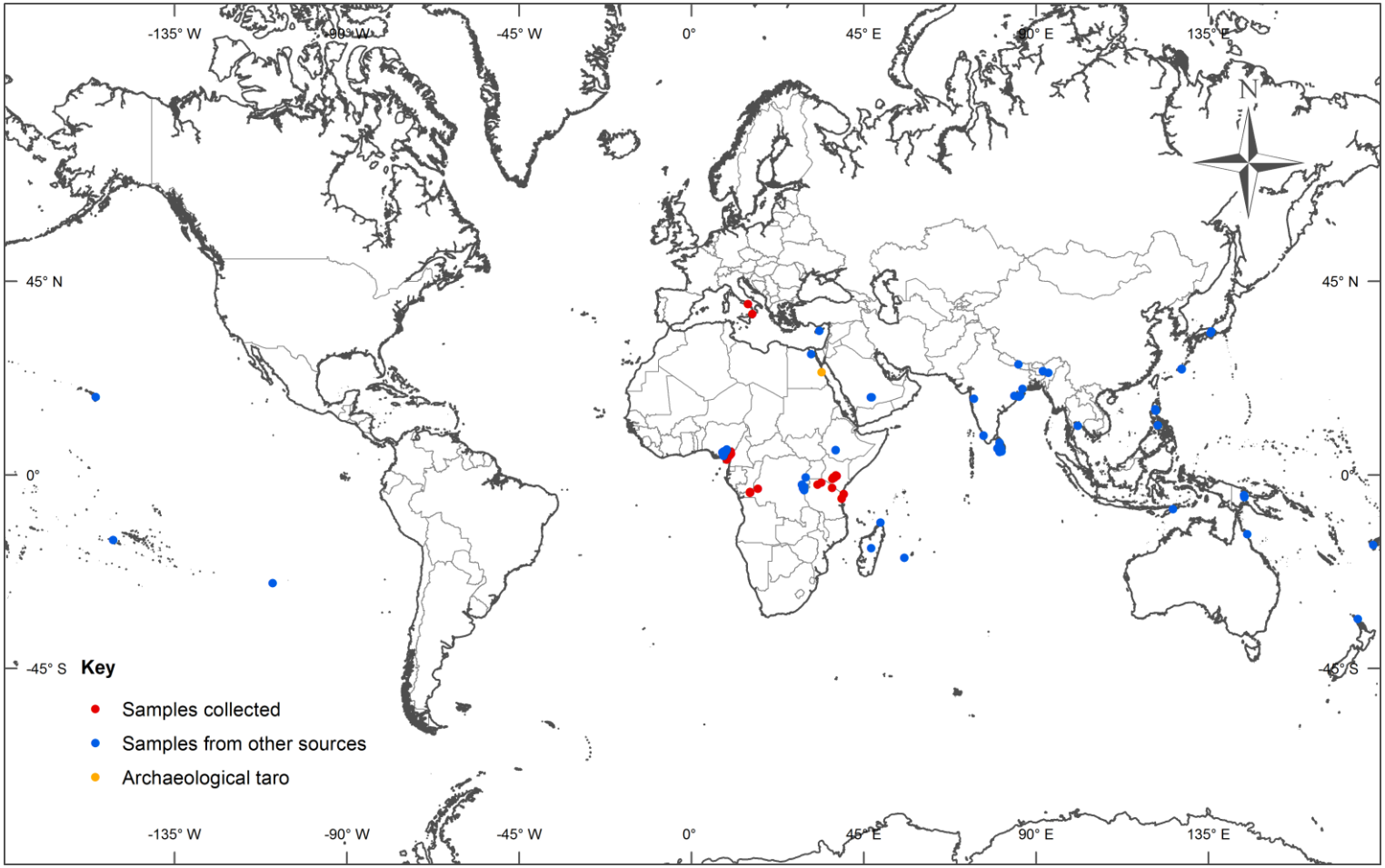


Figure 8. Map of Colocasia specimen collection used in this study. Red dots symbols represent sampling sites covered by the author. Blue dot symbols represent sampling sites covered by third parties.

CHAPTER 4 ETHNOBOTANICAL OBSERVATIONS

INTRODUCTION

Until recently, the representation of taro (*Colocasia esculenta* (L.) Schott) in African literature was restricted to a small number of nutritional (Tagodoe and Nip, 1994; Lewu et al., 2009) and medicinal studies (Lindsey et al., 2002; Nassr-Allah et al., 2009; Idu and Onyibe, 2007). Ethnobotanical research appears to be limited to some observations on taro in Nigeria (Ofori, 2003), South Africa (Shange, 2004; Mare, 2006), Kenya (Maundu et al., 1999), and single study of traditional cultivations of taro in Ethiopia (Fujimoto, 2009). This contradicts the knowledge that taro is a staple crop in West Africa and that is an invaluable resource for small-scale farmers (Ofori, 2003). One objective of the present research is to review scattered reports on taro in Africa, and the author's own field observations, in relation to morphological diversity, cultivation practices, culinary uses, and in general the traditions and indigenous uses associated with the plant. While collecting taro leaf specimens for genetic analysis, ethnographic observations in four selected countries of Africa were also made. The study was carried out from January to April 2010 in the Democratic Republic of Congo (DRC), Cameroon, Kenya and Tanzania.

During the fieldwork, informal interviews with farmers and researchers were conducted. The results of this fieldwork and the data collected will be

outlined in this chapter.

Firstly, a morphological description of taro is going to be given in order to familiarise the reader with the plant. This will be followed by observations gathered in West Africa, starting from the survey conducted in the west region of the Democratic Republic of Congo, followed by the survey carried out in Cameroon. Next, observations on taro in the east part of Africa will be summarised. The Kenya survey will be discussed first, followed by the survey conducted in Tanzania.

Figure 4 at pag. 54 shows the locations where the ethnographic study was undertaken and where taro leaf specimens were collected. A glossary of African terms and names has been compiled to assist readers of this document (Appendix 4). Terms found in the appendix will be highlighted in bold in the first instance, after which they will be written in standard font.

MORPHOLOGICAL DESCRIPTION OF TARO

Colocasia esculenta belongs to the family of Araceae also known as the Arum family. This taxon comprises 106 genera and 2,823 species (Govaerts and Frodin, 2002) distributed worldwide in temperate as well as tropical regions. They are characterized by an inflorescence, the spadix (Figure 38 to Figure 41 pag 119), often surrounded by a large bract called spathe. The spadix is composed of an upper part with sessile male flowers and female flowers at the base (Figure 40). When pollination occurs, they produce fruits as berries with tiny seeds, which are very rare in nature (Plucknett et al., 1970). The leaves are of a heart-shaped form and can reach large size (Figure 9). Even though the leaves show a variable morphology, they have a peltate structure where the petiole is attached to the central lower surface of the leaf (Figure 10). This is a useful character used to distinguish *Colocasia esculenta* from other similar aroids, particularly *Xanthosoma sagittifolium* that has the petiole junction attached to the edge of the leaf, usually in a sagittate structure. *Colocasia*, as with all the other aroids, has corms. On the basis of the corm morphology, Purseglove (1972: 61) recognised two botanical varieties, one that is known as eddoe (Figure 17 and Figure 18), and the other one as dasheen (Figure 23). Eddoe is said to be an African word, and a plant with this name was reported by Winterbottom (1803: 64) to have been introduced by Nova Scotia settlers in Sierra Leone. These were Afro Americans who, for political reasons (Walker, 2002), had migrated from Nova Scotia to Sierra Leone, and brought with them

samples of taro. Dasheen, instead, seems to be derived from Taro de Chine (Taro of China) that eventually became de Chine and so dasheen (Young, 1917) and it is characterized by having a main large edible corm and smaller corms aside.

AFRICAN TARO SURVEY

In Africa, as in other regions, taro is known by many different names in different contexts and languages. *Taro*, *cocoyam*, *dasheen*, *eddoe*, are names commonly used in the research literature on taro in Africa, and also have vernacular usage. While *eddoe* and *dasheen* remains unknown to most farmers and local people in Africa, the Polynesian name taro is used in the Democratic Republic of Congo, and *cocoyam* is the main name for taro in West Africa. *Nduma* and *majimbi* are common names for taro in the Kiswahili languages of Kenya and Tanzania respectively. To avoid confusion and to be consistent with other chapters in this thesis, the term **taro** will be used with its cognates only being listed where appropriate. Many of the names recorded are also applied to yautia (*Xanthosoma sagittifolium* (L.) Schott), a New World aroid also cultivated for its starchy corms, which is similar in appearance and often confused with taro. Morphological features of the leaf blade allow these two plants to be readily distinguished. The leaves of taro are usually peltate, with the leaf stalk (petiole) attached to the centre of the lower surface (Figure 9 and

10), rather than at or near the margin as in yautia.

Figure 9. Taro leaf specimen with the typical peltate structure.

Figure 10. Rear view of a taro leaf. Note the peltate structure.

Although yautia was not the primary target of this research, its history is likely to have had an impact on the use, abundance and movements of taro in the last two centuries. It was important, therefore, to identify and collect information about both taro and yautia. In *Agriculture en Afrique tropicale*, Raemaekers (2001) discusses both *Colocasia* sp. and *Xanthosoma sagittifolium* (L.) Schott in the same chapter. It is not uncommon to find the two plants treated as equivalent in the literature and in the field, though yautia is known to have greater tolerance of drought, and different culinary properties.

While collecting samples in West and East Africa, the social and environmental circumstances of taro proved to be very different. The surveys in both regions are outlined next.

OBSERVATION OF TARO IN WEST AFRICA

The survey in West Africa included the Democratic Republic of Congo (DRC) and Cameroon. A trip to Nigeria to visit the National Root Crops Research Institute (NRCRI), Umudike, Abia State had been previously scheduled, but due to an unstable political climate in the country, the visit was cancelled. Nevertheless, Mr Israel Borokini, from the National Centre for Genetic Research And Biotechnology NACGRAB (Ibadan, Oyo State, Nigeria) collected leaf samples and ethnographic information on our behalf. His contribution is significant to the improvement of knowledge of taro in Africa and it will be outlined in the course of this chapter.

SURVEY OF TARO IN WEST DEMOCRATIC REPUBLIC OF CONGO

In the DRC, the capital Kinshasa and the adjacent Bandudu province were surveyed in January 2010. Kinshasa, located on the south bank of the River Congo, has a population of almost nine million (UNSTAT, 2011) and represents an important hub for trading goods originating from all over the DRC and beyond. Goods are exchanged by ferry with Brazaville (the capital of the Republic of Congo), which is on the north bank of the river, providing a probable trade route for items to be exchanged including taro. In this region the term *taro* is applied by people, without distinction, to plants of yautia as well as to *Colocasia esculenta*. While taro is an English name adopted from the Polynesians, it is pronounced with a French accent. The cultivation of yautia is

more common than taro.

Although French is the official language, by government decree, four other national languages are used in the DRC: Lingala, spoken in the Kinshasa province, Kikongo in the Bandundu province, Tshiluba in the Kasai province and Kiswahili spoken in Eastern Congo. In Lingala, taro is called **malamakòkolo** where **mala** generally means corm and **kokolo** means leaf. However, since taro is often confused with yautia, this terminology can be applied to both plants as previously noted. In fact, mala is also said to be the term used for igname or yam (*Dioscorea alata* L.), therefore representing a general term for edible 'roots' of starchy root crops. Yautia is also known as **makabo** in Lingala, and **lupenzu** in Kikongo. For the most part, people do not recognise linguistically that yautia and taro are different. Instead, their main concern appears to be the difference between wild plants, some of which they consider bitter and toxic, and cultivated ones, which are thought to be edible and easy to cook.

In this area, the population usually consume yautia, and cassava (*Manihot esculenta* (L.) Crantz), and use both to make ***fufu*** - the typical paste made by pounding corms after boiling them until they reach the desired texture. This paste is consumed as a type of bread base, to which tomato sauce, vegetables, meat or fish are added. Taro appears to be used to a greater extent in the eastern part of Congo, where its corms are also used for making *fufu*. This may reflect regional differences in food preparation, and/or in the ease of

growing taro (the eastern part of Congo is wetter). The specimens that grow in the east are morphologically and agronomically different from those that grow in the west of the country. In the east, taro may have been introduced from bordering countries such as Uganda, Burundi, Rwanda and Tanzania. In Kinshasa, along the large main roads built during the colonial period (1867 to 1960), it is not uncommon to find uncultivated ditches filled with rainwater where plants of taro are left to grow wild (Figure 11 and 12) along with other edible plants which include, among others, sweet potato (*Ipomoea batatas* (L.) Lam.), and yautia. According to people that live in the area, taro is not normally consumed as food, but it is instead considered to be a medicinal plant used to cure burns. It is also generally known as "flower", a term used to indicate a decorative or nor-utility plant, because of its tendency to cause an itching sensation to the mouth and throat. The recognition of taro by such names was not unique to this area; it was also found in Kenya (see later). Even if not plentiful, flowering by taro is seen at the end of the rainy season (April and May), after which the plants lose their leaves. For those interested in gathering the corms, the changes in foliage indicate that the corms are ready to be harvested. The leaves are said to be so itchy that the feeling is similar to a sharp knife, this being the main reason why they are not used as food.

Other taro plants were found in the environs of Kinshasa in the garden of the University of Jesuits Saint Pierre Canisius (Faculté de Philosophie Saint Pierre Canisius), which shares part of its grounds with the Agronomic Institute

(Institut Superieur Agro-Véterinaire Saint Pierre Canisius). At this location, taro is not used for human consumption because the corms are too small and acrid. Compared to those plants found in the city, the ones found here are quite tolerant of dry conditions and hence are left to grow untended in the garden (Figure 13 and 14) and sometimes used as fodder for pigs. Generally speaking, in the west part of the DRC, other crops such as cassava or maize (*Zea mays* L.) are substituted for taro because of the ease of cooking and superior taste, the latter being considered a minor crop.

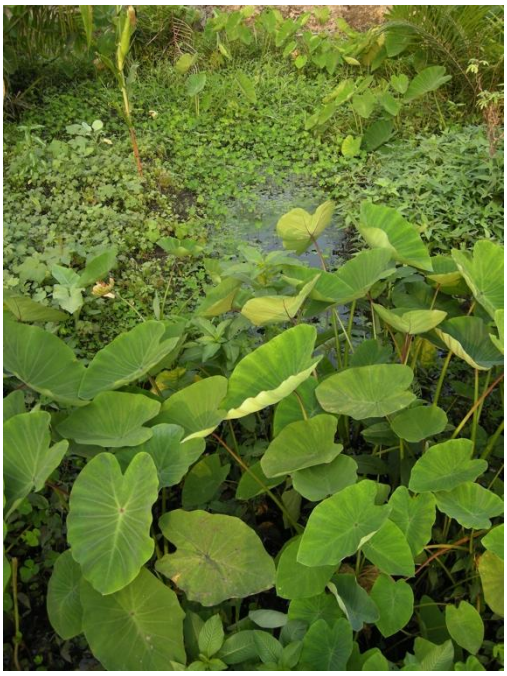


Figure 11. Taro plants growing along the road in Kinshasa (17th January 2010).

Figure 12. Corm of taro growing along the road in Kinshasa (17th January 2010).

Figure 13. Taro growing in dry soil in Kimwenza (18th January 2010).

Figure 14. Corm of taro growing in Kimwenza (18th January 2010).

From Kinshasa the survey continued to Kikwit, which is the biggest town in the Bandundu Province. From Kikwit we travelled to Kisandji, a small village in the Bandundu province, but located 800 km to the southeast. Although the area of this village is characterised by a grassland savannah-type environment, it was possible to find plants of taro on the way back to Kinshasa at ca. 350 km from Kinshasa, in a village called Kwango. This small village lies adjacent to the motorway that leads to Kikwit. The village takes its name from the River Kwango, a tributary of the Kasai River, which is one of the largest navigable water systems in Congo. In Kwango, subsistence agriculture predominates and taro is left to grow uncultivated in natural ponds together with banana and plants similar to *Lasiomorpha senegalensis* Hay (Figure 15) (identified by Peter J. Matthews). This plant is another member of the Araceae

family. Its presence and use in the countries visited is limited. In this area, Kiyaka is the local dialect and taro is known as **maniangu**, whereas *Lasiomorpha senegalensis* is called **langa.** The corms of *Lasiomorpha* are also known as langa, and this name is sometimes also applied to the corms of taro and yautia.

Figure 15. Pond with plants of *Lasiomorpha senegalensis* Hay (Kwango, 20th January 2010).

Beyond Kwango, no taro plants were seen, but yautia was cultivated as fodder for pigs, the reason given being that their corms are too acrid to be eaten even after being cooked for hours. The lack of taro cultivation could be related to the drier environment, but it could also be due to agricultural practices. Although Kikwit lies next to the banks of the river Kwilu, which

could provide a suitable environment for growing taro, the plant did not appear to be known locally.

During an earlier trip conducted by the author to the east part of the DRC during the summer of 2008, taro cultivations were seen, especially in the area near Lake Tanganyika (Figure 16) and Lake Bukavu. This is one of the poorest regions of the DRC where the lack of infrastructure, agricultural knowledge and technical skills hamper the development of a stable farming system. Nevertheless, abundance of water, during both the wet and dry seasons, allows taro to be cultivated with little effort in home gardens and along the banks of streams or natural perennial ponds. Here, taro represents a daily resource. The boiled corms are pounded to produce *fufu*.

To conclude, in the western DRC, taro is not commonly used as food for people, but it is known as a medicinal plant to cure sores or burns. The main diet includes processed maize and cassava that are used to produce *fufu*, a typical paste made to accompany vegetable and meat sauces. In the eastern DRC, taro is sometimes used as food in the daily diet, but when available cassava is preferred as it is easier to cook and more appealing for local taste.

Figure 16. Taro and yautia plants growing on the shores of the Lake Tanganyika (Uvira, 8th August 2008).

CAMEROON

In Cameroon, as in the DRC, taro often grows together with other members of the Araceae family: *Alocasia* sp. and *Xanthosoma spp.* It is also common to find water yam (*Dioscorea alata* L.) growing in the same environments. Taro, yautia and water yam are root crops that have excellent nutritional properties and represent a safe and economic resource for the population, which strongly relies on them for small to medium scale cultivation. The climate of Cameroon is generally tropical, and relatively wet in the southwest. Bananas and plantains (*Musa* spp. L.), mango (*Mangifera indica* L.), papaya (*Carica papaya* L.), and avocado (*Persea Americana* Mill.) are all grown. Large parts of the territory are also covered in rubber tree (*Hevea brasiliensis* (Willd. ex A.Juss) Müll. Arg) and oil palm (*Elaeis guineensis* Jacq.).

In Cameroon a greater range of taro cultivars was seen than in the DRC. The crop is increasingly becoming a staple food for a population that has seen a dramatic drop in harvests of other major crops (e.g yautia) (researchers' pers. comm.). Depending on the region and variety, the plants have different names. The main local variety is known as **country coco**, which has a purple petiole colour, small and soft white corms, and tolerance to dry soil conditions (Figure 17). Having smaller and many side-corms, the country coco type fits the description of the botanical variety known as **eddoe** or var. *antiquorum* (Purseglove, 1972) (Figure 18).

Figure 17. Country coco in Cameroon (Bafoussam, 6th February 2010).

Figure 18. Corms of country coco (Buèa, 3rd February 2010).

Another cultivar is known as **mangua** or **mantan** (depending on the

local dialect), a name for which the etymology remains obscure. This variety has large leaves, long off-white stems (Figure 19), and a large reddish skin corm surrounded by smaller ones (Figure 20). The mangua type also appears to be the botanical variety known as **dasheen** (Purseglove, 1972), though this nomenclature changes in different regions (Plucknett, 1983).

Figure 19. Specimen of Mangua cultivar (Bamenda, 7th February 2010).

Figure 20. Corms of the mangua type (Buéa, 3rd February 2010).

A third variety is known as **Igbo cocoyam** (pronounced Ibu cocoyam). This variety takes its name from a Nigerian tribe that is thought to be responsible for its introduction to Cameroon. Two types of Igbo cocoyam are said to have been introduced: one has a greenish petiole (Figure 21) and a single elongated corm generally known as "taro of the river" (Figure 22); the

second has a reddish colour on the upper petiole (Figure 23) and corm shape resembling the dasheen morphotype (Figure 24). The corm is never as large as that of mangua, with the texture being tough and its skin often quite thick. According to local informants, people mix it with other types of corms, as they are not inclined to chew it. These two types of taro do not produce flowers at any stage in their life cycle (local farmers' observations).

Figure 21. Igbo cocoyam in Cameroon (Bamenda, 7th February 2010).

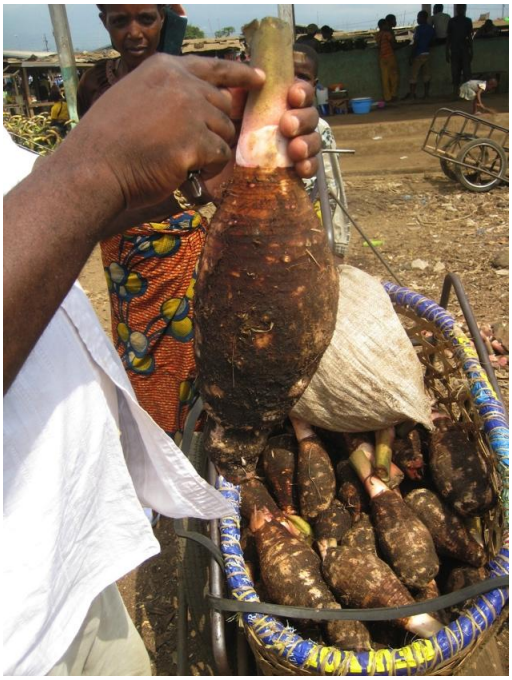


Figure 22. Corm of taro of the river (representing also the dasheen morphotype) (Buéa, 3rd February 2010).

Figure 23. Igbo cocoyam (Bamenda, 7th February 2010).

Figure 24. Dasheen type (Buéa, 3rd February, 2010).

In this region of Cameroon, it is a common practise to burn stacks of brush and leaves to fertilise the soil in order to improve taro yield, with

cultivation generally following a crop rotation system. At the beginning of the rainy season, potato plants are harvested shortly before the planting of taro, which is usually planted alongside maize. Since maize normally reaches maturity before taro, it is harvested promptly so as to give taro a last boost for corm production (by reducing competition). In September, at the end of the rainy season taro plants start losing their leaves, and a month later the corms are ready to be harvested, after which they are often left in the field under raffia palm leaves (*Raphia* spp. P.Beauv.). This easily arranged storage inhibits rotting prior to corms being sold at market in the following months. Taro corms are known to start rotting as early as two weeks after being removed from the ground, and that after a further six months storage the yield is often reduced by 90% (Njintang and Mbofung, 2003b), a major problem in post production systems and a reason for not farming taro in other areas (Minagri, 1999 in Njintang and Mbofund, 2003b).

PEST ATTACK AND TARO LEAF BLIGHT

Pest attacks are not uncommon, but pesticides are not routinely used. According to Xavier Ndzana (Institute of Agricultural Research for Development, IRAD-Cameroon), a fungal attack of yautia plants in 2009 resulted in a critical loss of yield, initiating prompt research into producing cultivars that are resistant to the pathogen. Taro plants were also affected by

the fungus, but it appeared that the losses were less than the more-utilised yautia. In particular, the mangua type seems to be more resistant to the pathogen infection (Xavier Ndzana pers. comm.). The fungal attack, that according to Xavier Ndzana was *Pythium myriotylum* Drechsler, was thought to have come from Ghana, where it has been previously reported in 1981 (Steiner, 1981). However, in this region the spread of another fungal pest, the *Phytophthora colocasiae* (taro leaf blight), was also noted by Guarino (2010), Bandyopadhyay et al. (2011), and Omane et al. (2012). According to Dr Leke Nkeabeng (IRAD-Cameroon, pers. comm.), the declining populations of local cultivars are likely to be replaced by resistant taro plants of Pacific provenance. At the IRAD-Cameroon, multiplication of new clones from the Pacific breeding programme is in progress.

MEDICINAL USE OF TARO IN CAMEROON

As in the DRC, where taro is seen broadly as a medicinal plant, its use in curing health problems was also noted in the area of Widikum. Here, informants reported that water deposited on the leaves of taro was collected and used to cure throat problems. It is not known if the leaves of taro in contact with water release particular chemicals that are beneficial for the throat. This may be a case of "sympathetic medicine"- water moves smoothly on the surface of a taro leaf and this might suggest its use to address problems in the

throat. A similar use was found in Kenya (see later).

CULINARY USE OF TARO IN CAMEROON

Taro is widely employed in Cameroonian cuisine. The leaves are sold in markets and can be used to prepare a dish known as **ekwang**, which consists of grated corms of yautia, sometimes with fish or occasionally with meat, which are wrapped in taro (only the country coco type) or yautia leaves to form dumplings, which are then placed in a pan of boiling water. After cooking (which removes acridity), they are ready to be served with a previously prepared sauce. The corms of taro are used to prepare ***Achu***, a typical dish of the country. This is a paste made by boiling and pounding corms of different varieties of taro, together with small local bananas that are used only in the preparation of this meal. The dish is sometimes accompanied with a yellow sauce prepared using limestone powder[2] and many spices, resulting in an extremely sour taste (this sauce is also used as a treatment for alcoholism). At the end of the wet season in June/July, some taro plants (country coco type) produce inflorescences from which a sauce is made. This produces a dark product called "black sauce" (Ejoh et al., 1996), which is eaten with vegetables and cow skin fat. For reference, a recipe to prepare the *Achu* is

[2] Limestone powder is claimed to have an inhibitory effect towards alcohol in beer and wine.

presented here.

Preparation of Achu

Ingredients:

For the sauce

Local spices (country onion, bush pepper, pepper, mpebe and others according to personal taste)
Local chilli peppers
Limestone
Stock
Salt
Palm oil

For the paste

Corms of taro (different varieties with different textures, soft and hard: country coco, mangua, igbo cocoyam)
Local bananas used only for the preparation of *Achu*, not to be eaten on their own.

Other

Leaves of yautia to cover the bowl while the corms and bananas are boiling
Leaves of banana to wrap the paste that will be used in the following week

A large pot is filled with the different varieties of corms, the special variety of banana is placed at top of the pot, and the contents are covered with yautia leaves that help to keep the corms simmering. The bananas are essentially used to give the paste the right texture (not too hard or too soft). Preparation takes between five and seven hours, depending on the amount of taro boiled and pounded — and the strength of those who pound the corms! When the paste is ready, it is divided and wrapped in small parcels with banana leaves. The parcels are then kept in a dry place. Since the preparation is long and laborious, the paste is prepared in large quantities that may last for at least a week. This also constitutes a food resource not only for a single family, but for others through sharing.

The sauce is prepared with limestone as a base. The preparation of the sauce starts by grinding spices, then mixing the resulting powder with ground chilli peppers. After this, water is poured into the limestone powder and added to the spice-chilli mix with palm oil and salt. The taste is very strong and sour.

EAST AFRICAN TARO ETHNOBOTANICAL BACKGROUND

In West Africa, taro corms are prepared using various methods and consumed as a daily food, but in East Africa this plant occupies a more minor role. Corms are sometimes cooked and used as a snack to eat together with tea (Figure 25). They are also fried and stewed with potatoes (*Solanum tuberosum* L.), or sometimes mashed or cut into crisps. In this region there is a visible cultural difference in the way taro is perceived. Traditional cultivations that are found in the Highlands deserve particular attention, as the crop is disappearing (farmers and researchers information).

Figure 25. Boiled corms of taro with tea and tea flask (Kakingo-Kiamworia, 18th March 2010).

KENYA

In Kenya, taro is generally known in Kiswahili as **nduma**, **induma** or **enduma** in Luhya, a Bantu language of western Kenya. This term is also

applied to yautia. The English name **arrowroot** is also used to indicate taro corms. Depending on variety and local dialect, farmers often use other names. In Kenya only one variety of taro was found being cultivated and consumed. But at field margins, other varieties are left to grow wild in case of food shortage (see next).

The cultivated variety is called **nduma ngirigaca** (Ngirigaca in Kiswahili means "agriculture") and is sometimes described as a **musungu** crop (*musungu* in Kiswahili means "white man"). Interviews conducted with farmers revealed that the *musungu* crop was brought by foreign agricultural officers in the 1940s to replace old cultivars that needed to be cooked for longer periods. This variety has red colouring in the upper petiole suggesting that it may be similar to the Cameroonian variety known as Igbo Cocoyam (Figure 26). As with the Igbo type in Cameroon, this variety is also said to never flower (by farmers). The corms are of a mixed white and reddish colour, and after being boiled, they become soft and are consumed with no further preparation. Täckholm and Drar (1941: 382) reported that a new variety was introduced under the name *Qolqas americani* and distributed by the Horticultural Section of the Ministry of Agriculture to Egyptian farmers. This variety was distinguished by the absence of mucilaginous matter that causes the itchy sensation around the mouth and throat. As a modern agricultural service introduction, the Kenyan variety might be the same as that introduced to Egypt. Closer study is needed of the plants and agricultural service records to determine if this is the case.

Figure 26. Farmers in their taro field. Note the red notch on the upper part of the petiole (Kakingo-Kiamworia, 18th March 2010).

In Kenya, other varieties that remain but are no longer cultivated, display small corms and high acridity. One of them is known as **muraria riko**, from the Kimeru term **muraria** that means "to keep someone awake" and **riko** that means "on the fire". It seems (from the following story) these corms can be eaten only after been cooked overnight on the fire (farmers' account). Women point out that before the ngirigaca variety was introduced in the last 70 years, their ancestors used to put some corms of this particular type of taro on the fire, and leave them overnight for men, who in the morning would eat them for breakfast. The muraria riko variety is no longer cultivated but it is still found in the fields. This variety has a greenish petiole.

Another variety is called **nyakigoi**, which means the plant "that sheds".

At the end of the growing season these plants shed their leaves, indicating that the corms are ready to be harvested. This variety is also no longer used. A third variety with white petioles is known in Kimeru dialect as **muthangari mwea**. It is usually very tall and it looks like the mangua variety (dasheen type) seen in Cameroon. The corms can be cooked in a relatively short time, and become tender and soft. To prepare a medicament for stomach problems, the leaves are boiled and then maize flour is added until the mixture becomes green. Once the concoction has cooled it is ready to be eaten.

Finally, among minor varieties some time grown for food, there is a fourth variety known as **mwanake,** that in Kiswahili means "young initiated man". This refers to the bitter taste of the corms, which only strong young men are able to eat, although people say that in reality it causes serious problems to the digestive system. It was rarely given to children because it was so irritating, but now the plant is used to cure cow tonsillitis. The medicament is prepared by washing and mashing 100-200 grams of raw corms in 1 litre of water. Once the big particles are removed, the remaining liquid is fed to animals. The leaves are also used to prepare bath water for women that have just given birth. These plants have purple stems (Figure 27) and small corms (Figure 28) and are known to flower. They appear to be of the eddoe type. However, mwanake is rarely cultivated and is consumed only in times of famine, as recalled in oral tradition (MacKenzie, 1986).

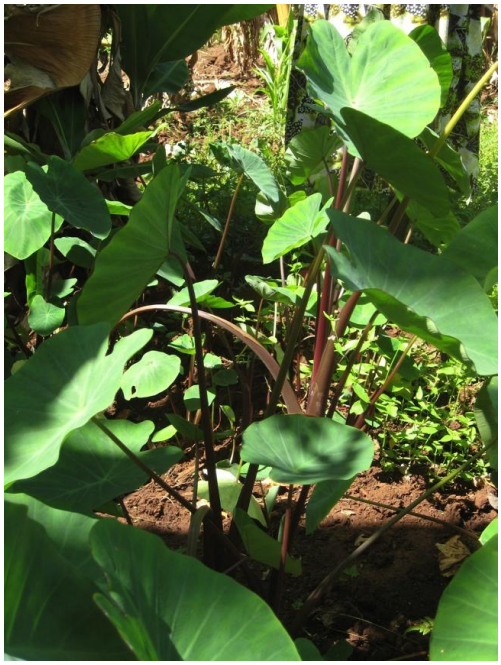


Figure 27. Variety of taro known as mwanake (Ena, 26th February 2010).

Figure 28. Corms of the mwanake variety (Ena, 26th February 2010).

In this country we found varieties of taro that are not widely used but had greater importance in the past. Older farmers recall the presence of a further variety in earlier times, and describe it as being eaten after long cooking in plentiful water. This plant has a greenish/brownish petiole and displays distinct enation alongside veins on the leaf under surface (Figure 29). Local people call this a "decoration". A similar trait was reported by Guéguen (1908) in at least one cultivar found at the University of Hawaii Agricultural Experiment Station. Strauss (1983) suggested that such an outgrowth is determined early in leaf development, and results from genetically controlled overgrowth of meristematic tissue. Matthews (pers. comm.) has also observed this trait in a New Guinea highlands cultivar.

Figure 29. Enations on the lower surface of a taro leaf (Meru, 3rd March 2010).

AGRONOMIC PRACTICES

In the region of Kenya surveyed, cash crops like coffee and maize occupy a central role in farming, but minor crops like beans, sorghum, and taro are also important for small-scale farmers. In Kenya, taro grows under rain-fed conditions at the bottom of valleys where perennial water flows also help it to thrive. Interviews with farmers revealed that the low valley cultivation is the result of intense deforestation of wet woodlands that occurred in the 1930s. Before that period, diverse taro varieties were in widespread cultivation. Subsequent deforestation caused the drying of fertile soils, and as a consequence taro production gradually migrated into the remaining moist ground found at the bottom of valleys.

Since cultivated taro is clonally propagated, the tops of harvested corms, with attached petioles are replanted, covered with soil and left to grow again (Figure 30 and Figure 31).

In the field margins, plants of *Brassica oleracea* L. are cultivated. In Kiswahili these are called **sukuma wiki** which literally means "push the week", a way to indicate a food used in times of scarcity. Farmers also plant sweet potatoes, onions, banana, sugarcane, mango, and papaya trees. The slopes of the valleys are generally infertile. For this reason farmers use the slopes to cultivate Napier grass (*Pennisetum purpureum* Schumach.), as a fodder for livestock.

Figure 30. Clonal propagation of taro (Meru, 3rd March 2010).

Figure 31. Petioles replanted for the following season (Meru, 3rd March 2010).

NATURALISED WILD TARO

As mentioned above, two naturalised varieties of taro were found in Kenya. The first was present in Maua, a small town in the Eastern province of the country. The plant has a dark (almost black) petiole and blade. The corms

of these plants are rather rudimentary and are considered toxic. The plants are regarded as decorative and known as "flowers". Due to unsafe political circumstances, it was not possible to interview people living in Maua. Four leaf samples were collected, but it was not possible to photograph them.

A second form of wild taro was found in marshlands where rice is normally cultivated (Figure 32). These plants display green pointed leaf blades, and dark green petioles (Figure 33). Local people were interviewed, but no information regarding use or provenance could be obtained.

Figure 32. Marshlands with taro plants (unknown location near paddy fields Kenya, 6th March, 2010).

Figure 33. Taro with pointed leaves growing in the wild (unknown location near paddy fields in Kenya, 6th March 2010).

CULINARY USES

In Kenya, taro corms are served as a snack as food. A common dish called **irio** or **mataha** is prepared by mixing the leaf blades of nduma ngirigaca

with potatoes, maize, cooked beans and plantains. After the mixture is well blended, it is mashed and shaped into dumplings that are cooked.

Compared to the DRC, taro occupies a role more important than yautia in Kenya. The leaves of yautia are never used for consumption, as they are considered poisonous. The corms are also treated carefully as people say that the mother corm is poisonous. The lateral cormels are used, but are not preferred or used for daily consumption.

TANZANIA

Even though Kiswahili is spoken both in Tanzania and Kenya, different words are used to identify taro. In Tanzania, depending on the area, the corms of taro are known as **maghimbi**, **magimbi** (also spelled as **majimbi**) or **magimbi poli**. Often it is referred to as **magimbi magi**, where **magi** in Kiswahili means "water", indicating that is a plant that grows in water. The leaves are known as mayugwa (Walsh, 2009). In East Africa cocoyam is also a vernacular term for taro (Talwana et al., 2009), though this was not used by the people encountered during the present survey.

The primary objective in Tanzania was to survey taro and collect samples in the Zanzibar Archipelago: Unguja and Pemba. These two islands, due to their historical roles as trading centres, are critical locations that could represent a portal for crops moving between Asia and Africa. The area is a

possible place of introduction for taro entering Africa. Local people referred to traditional cultivation of taro in the area near Morogoro, a city located in the southern part of Tanzania. Due to unforeseen circumstances it was not possible to survey this area. Generally speaking, taro does not seem to be widely cultivated or consumed in Tanzania. Cultivations of taro were rare. Plants were more often seen growing wild in dumps, along drainage systems, or in swampy areas, all in the vicinity of Lake Victoria.

On the island of Pemba there was only one type of taro with a red colouring in the upper petiole (Figure 34). Morphologically, this plant resembles the Igbo cocoyam found in Cameroon and the nduma ngirigaca found in Kenya. A similar plant was seen and collected in the area nearby Lake Victoria in Tanzania. In Pemba, people do not seem to appreciate them, since they were often removed and burnt in order to accommodate other crops "in the past" (local informant).

In Unguja at least three taro varieties were evident: one with a red petiole, (Figure 36), one with green petiole and green blades, and a third with dark petiole (Figure 37). With a strong Arabic influence (Figure 35), Tanzanian cuisine is imbued with sweet flavours and hence taro is eaten boiled in coconut milk which gives the corms a sweet and delicate taste. In this country two plants were seen in flower, and pollen was observed (Figure 39-41).

Figure 34. Taro variety in Pemba (19th March, 2010).

Figure 35. Plants of taro in front of a mosque Pemba, 20th March 2010).

Figure 36. Variety of taro (dasheen type) in Unguja, 16th March 2010).

Figure 37. Other variety of taro in Unguja, 16th March 2010.

TARO FLOWER

Figure 38. Inflorescence of taro. Arusha, 25th March 2010.

Figure 39. Detail of taro inflorescence. Arusha, 25th March 2010.

Figure 40. Female zone inside the lower spathe (green area). Arusha, 25th March 2010.

Figure 41. Sterile appendage at right of arrow, and male flower zone at left, with pollen realised. Arusha, 25th March 2010.

NOTES ON YAUTIA IN TANZANIA

In Tanzania yautia is said to produce numerous corms compared to the single corm of the taro plant, and is therefore preferred for cultivation because of its greater productivity. Furthermore, chemical composition studies carried out to analyse the proximate (water content, crude fat, nitrogen, ash, total carbohydrates, etc.) and mineral content of taro and yautia (Ndabikunze et al., 2011) showed the much greater nutritional value of yautia compared to taro. This result is in line with research exploring the different composition of taro and yautia in Nigeria (Sefa-Dedeh and Agyir-Sackey, 2004).

CONCLUDING REMARKS

The purpose of the fieldwork carried out in Africa was to collect leaf samples and information related to the use and perception of taro in local cultures. Four countries located on the Equatorial belt were surveyed: the DRC, Cameroon, Kenya and Tanzania. A total of 491 leaf samples were collected, but flowering was seen on only two occasions. Yautia is a New World aroid that is found in association with taro; they are similar plants and people often use the same name to describe them. This convergence of names can cause confusion in sample and data collection, but the plants are easily distinguished by leaf morphology. Since the leaves were targeted for sampling, there was no confusion in the present survey.

Regarding the food value attributed to taro, a geographical distinction

between West and East Africa is apparent. In the DRC taro is not often consumed as food, but it is rather considered a poisonous plant with some medicinal properties to cure burns and plagues. In Cameroon, taro is a staple crop and is fully part of the local food culture. The corms are the part that is mainly consumed as food to prepare the *Achu*, a typical dish made by pounding corms and cormels of taro. Medicinal use of the blades was also recorded. In East Africa, taro occupies a minor role and is often considered an emergency crop to be used in case of food shortage. The corms are consumed as a snack to be eaten for breakfast, but a more refined taste is given when cooked with coconut milk. The corms are also employed as a medicine to cure animals' tonsillitis.

Several varieties of taro were observed and described in each country visited. Some of them show a high acridity (by reputation), but one variety seems to be commonly cultivated and to have replaced other minor varieties. This plant has a distinctive red colour of the upper petiole (and main veins of the rear lobes of blade), and has low acridity, which facilitates its cooking. The plant is known as *Igbo cocoyam* in Cameroon, and in Kenya as *nduma ngirigaca* or *musungu crop*. In Tanzania, there is no specific name for it, but it is simply known as *magimbi magi*. According to Kenyan farmers, white agriculture officers introduced this variety in the 1940s in order to replace local varieties that were highly acrid and only edible after being cooked for a long time.

CHAPTER 5 GENETIC RESULTS

INTRODUCTION

The aim of this chapter is to detail the characterisation of chloroplast and nuclear variation of the taro samples collected and analysed during the course of this study. In particular, the objective of the nuclear DNA work is to describe nuclear DNA allelic and genotypic diversity in taro samples collected in Africa. A comparison with samples of taro sourced elsewhere by third parties will also be drawn.

In the first part of the chapter the results of the genetic analysis will be outlined, first by looking at the investigation of the chloroplast genome, and then by analysing the DNA variation of selected nuclear microsatellites. In the second part, the genetic research carried out on archaeological taro will be summarised and the results discussed.

DNA EXTRACTION and PCR AMPLIFICATION

In this study, 739 leaf specimens were collected and successful DNA extraction was performed. Six of these samples were known to belong to other species (Table 9) and were used to investigate the relationships at chloroplast level with the specimens of *Colocasia esculenta* collected in Africa and elsewhere.

Table 9. Samples used as outgroups.

Sample ID	Place of collection	Notes
32.1	Japan	*Colocasia gigantea* (Blume) Hook.f.
32.2	Taiwan	*Colocasia formosana* Hayata
TG1	wild origin	*Remusatia vivipara* (Roxb) Schott
TG2	N/A	*Colocasia affinis* var Jenningsii
TG3	Taiwan	*Colocasia formosana* Hayata
TG38	Sri Lanka	*Colocasia fontanesii* Schott

Of the remaining 733 samples investigated, 40 failed PCR amplification, leaving a total number of 693 samples for use in this research. Failure in the amplification of selected loci can be attributed to several factors, of which two are worthy of mention. The first aspect to be considered is that the analysis of microsatellite loci is generally species-specific, and even though closely related species are likely to amplify due to the fact that their primer regions are still conserved, long time divergence between organisms increases the mutation in the primers region, thus affecting the percentage of failure in PCR amplification. In other words, microsatellite primers were designed on species of *Colocasia esculenta* (Mace and Godwin, 2002), and the great antiquity of the

tribe Colocasieae is likely to have diverged at the loci. The second factor which may have led to issues with amplification is an inadequate leaf drying process. Some leaf samples collected by third parties were still wet when received; in order to preserve the nucleic acid, plants must be dried under optimum conditions, which if not carried out will result in poor DNA extraction and the consequent failure of the amplification process. Rapid drying method with silica-gel is suggested for best preservation of DNA material and consequent achievement of high molecular weight DNA. Table 10 lists the samples that failed in this way.

Table 10. Samples that failed PCR amplification in all the loci investigated.

Sample ID	Place of collection	Notes
SRI 1.4a; SRI 1.4b	Sri Lanka	*Alocasia* spp.
UV 3.1; UV 3.2; UV 3.3	Uvira (DRC)	
UV 4.1; UV 4.2; UV 4.3	Uvira (DRC)	
UG 1.2; UG 1.3; UG 1.5;	Uganda	
32.5	Japan	*C. esculenta* cv Dodare
37.8	Sri Lanka	
47.2; 47.3; 47.4; 47.6; 47.7; 47.10; 47.11; 47.12; 47.37; 47.41; 47.44; 47.45; 47.49; 47.50	Nigeria	Wet samples
44.1; 44.4; 44.6	La Réunion	*Xanthosoma*
TG10, T32	PNG	
TG14; TG24	Philippines	
TG40	Thailand	
DM1.3; DM2.4; DM2.5; DM2.8	Assam (India)	

CHLOROPLAST DATA

The use of chloroplast markers to reconstruct phylogenetic relationships at population level is limited by low resolving power (Provan et al., 2001). However, Ahmed et al. (2013) have recently characterized additional suitable chloroplast loci to investigate phylogenetic relationships within the genus *Colocasia* as well as in other plant groups. These markers were not available at the beginning of this study and therefore could not be used.

Other chloroplast regions were available and were used for rapid and accurate species identification (Taberlet et al., 1991). In this study two chloroplast regions were investigated with the results summarised as follows.

TRNL INTRON

The amplification of the *trn*L intron region, performed with the use of highly conserved primers *a* and *b* (Taberlet et al., 1991), resulted in a product of 1205 base pairs. Primers *e* and *f* (Taberlet et al., 1991) were also successfully tested, which resulted in the amplification of a product of 454 nucleotides. However, initial tests showed low-resolving power of these loci, as confirmed by Taberlet et al. (2007), which is the reason why these markers were avoided in this study.

The *trn*L intron with primers *c* and *d* was also amplified successfully. In order to investigate the nature of the region sequenced, tests were performed

on selected samples. For each of these samples, the results of the sequencing gave unreadable sequences. This is most probably due to a long series of adenines A and thymines T that are located in the selected region and that cause the DNA polymerase to slip, thus resulting in non-readable sequences. This issue was highlighted in Renner and Zhang (2004) and the use of this marker was therefore avoided in this study.

TRNK INTRON

In view of the issues described above, a segment of 314 base pairs located within the *trn*K intron region was chosen to perform the analysis using the chloroplast molecule. The analysis of this segment in both modern and ancient material revealed one single SNP A/G, thus dividing the 693 samples in two groups. When DNA sequences were subject to a BLAST search against the NCBI nucleotide database, it showed that they belonged to two taro chloroplast DNA genotypes as characterized in Ahmed et al. (2012).

These two different chloroplast types were named *C. esculenta* var. RR, an acronym derived from *Red* petiole and *Rounded* leaf blade, and *C. esculenta* var. GP, the acronym in this case coming from *Green* petiole and *Pointed* leaf blade (Matthews, 1985). However, the GP and RR type should not be seen as a genetic characterization associated with specific morphological characters. In fact, the plants observed during fieldwork showed a mix of morphological

characters and therefore were characterised by extensive morphological variation.

The SNP in question is found at position 233 counting up from the forward primer: in the GP type there is an adenine A, and in the RR type a guanine G. The results show that from a total number of 693 plants, 262 are of the GP associated type and 238 of the RR associated type, with the remaining 193 samples failing PCR amplification at this locus.

Sequences of the GP type and the RR type were aligned with close species of *Colocasia esculenta* which were received during this study and that were treated as outgroups. By considering the character states and relationships of outgroups, one can estimate the ancestral state of a specific group. In particular, sequences of *Alocasia* spp., *Remusatia vivipara*, *Colocasia affinis* and *Xanthosoma* spp. sequences were used to construct a phylogenetic tree using Maximum Parsimony with 10,000 bootstrap replicates using MEGA 5.2.1 (Tamura et al., 2011). The resulting tree is shown in Figure 42.

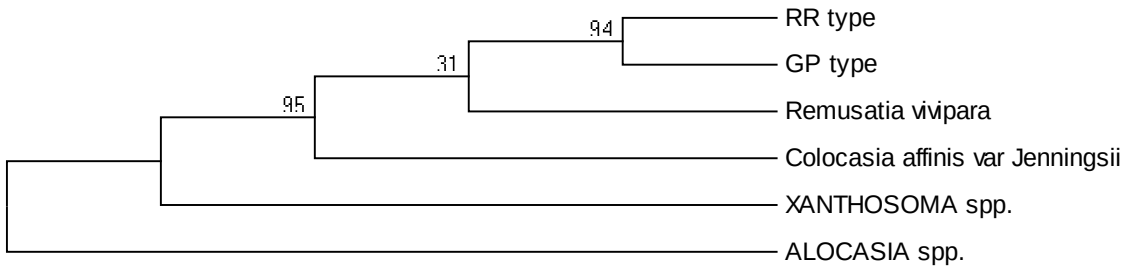


Figure 42. Maximum parsimony tree with 10,000 Bootstrap values.

The tree obtained from chloroplast sequence characters in *Colocasia esculenta* and outgroups shows that *Alocasia*, *Xanthosoma*, *Colocasia affinis* var

Jenningsii, *Remusatia vivipara* and *Colocasia esculenta* RR contain the nucleotide substitution guanine G, while *Colocasia esculenta* GP is the only sample that showed the nucleotide substitution adenine A. This result seems to suggest that the RR type is the plesiomorphic (primitive) state, and the GP lineage is the synapomorphic (derived) that diverged from the main Aroid phyletic line.

While research on taro chloroplast is still ongoing, a comparison with the work carried out by Ibrar Ahmed under the supervision of Prof Peter J. Lockhart and Peter J. Matthews at Massey University, New Zealand, was made very recently. The comparison between selected African and Asian genotypes revealed that taro present in Africa is likely to belong to two of three different clades that have recently been identified by the New Zealand team in taro collected in several parts of Asia (unpublished). Based on a comparison with their findings, one group of plants that are found in Africa seems to belong to a subclade in which South Asian tropical diploid and triploid taro cultivars are included. The plants that belong to this group are found in the Mediterranean region (Italy, Cyprus, Egypt), in Nigeria, in Cameroon (Bafang, Bamenda and Limbe), in Kenya (Murang'a) and in Tanzania (Arusha) (Figure 43).

The second group of plants that are found in Africa seem to belong to a clade of cool-adapted triploid cultivars, possibly of Himalayan origin. This type of plant corresponds to the eddoe phenotype (Figure 17 and Figure 18 Chapter 4, pag. 100) which is reported to be dominant in Ethiopia and Africa

generally (Fujimoto, 2009). This observation is confirmed by the research carried out in Africa, in which this plant appears to be the most frequent genotype found across all Africa from east to west. Interestingly, the African plants that seem to belong to the triploid cool adapted group do not show three allelic forms at any of the three loci investigated. Figure 44 shows the distribution of this variety of taro.

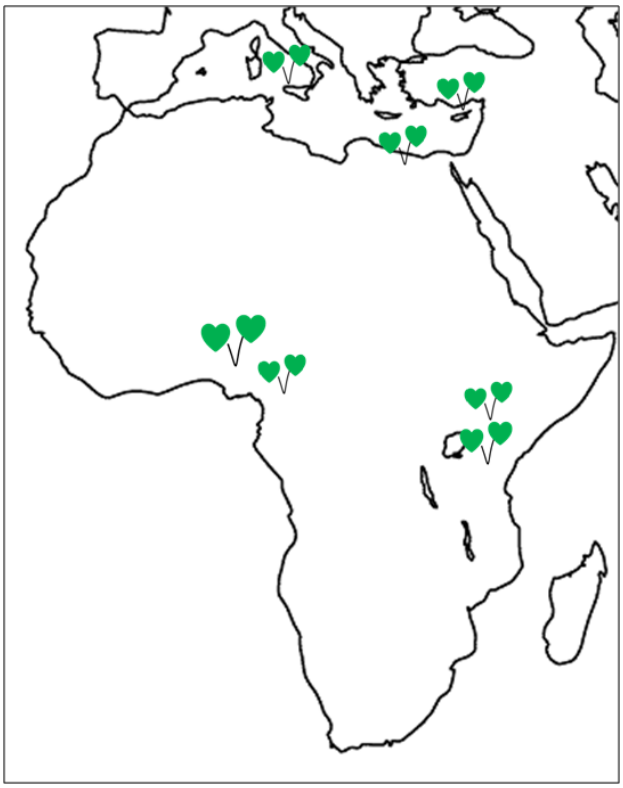


Figure 43. Distribution of samples corresponding to the South Asia diploid and triploid group identified by Ahmed (unpublished).

Figure 44. Distribution of taro samples corresponding to cool-adapted triploid cultivars of probable Himalayan origin identified by Ahmed (unpublished).

MICROSATELLITES DATA AND TREE

NUCLEAR MICROSATELLITE MARKERS SELECTED

In order to analyse the genetic variation and relationships of taro in Africa, investigation of the nuclear genome was also undertaken. A total of 10 nuclear microsatellite loci were selected for this study. More specifically, eight markers were selected from Mace and Godwin (2002) and two more from Hu et al. (2009). These molecular markers were chosen according to their nucleotide composition, polymorphism, and electrophoresis pattern. Markers selected and tested in this study are reported in Table 11. In order to assess the quality and performance of these markers, PCR amplification tests without fluorescent labels were first performed on a smaller set of samples representative of the entire geographical area studied. In particular, peak scoring and loci polymorphism were taken as indicators.

In the preliminary test locus Xuqtem247 and Xuqtem249 repeatedly failed amplification of single products even when different temperatures and MgCl2 volumes were tried. These markers were therefore deleted from the analyses. Xuqtem55 amplified successfully, but the bands produced showed blurred borders rather than a single sharp one, suggesting stuttering behaviour during PCR amplification. Stutter bands are quite common in microsatellites. During replication, depending on the nature of the microsatellite and its nucleotide composition, slippage of the DNA

polymerase can occur backwards or forwards, resulting in the production of amplicons of different lengths that obscure the real nature of the genomic region being investigated. Locus HK7 selected from Hu et al. (2009) was not included because of limited funding in the later stages of data extrapolation.

Table 11. Markers selected in this study.

SSR locus	Repeat motif	Annealing T °C
Xuqtem55	$(CAC)_5$	62
Xuqtem84	$(CT)_{18}$	62
Xuqtem88B	$(CAT)_9$	60
Xuqtem91	$(TG)_6(GA)_4$	56
Xuqtem110	$(TGA)_6(TGGA)_4$	55
Xuqtem132	$(TTTGAA)_4$	55
Xuqtem223	$(CTT)_9$	55
Xuqtem228	$(GAA)_5$	60
Xuqtem247	$(CT)_{10}$	N/A
Xuqtem249	$(AG)_{10}$	N/A
HK7	$(CT)_{14}TTCTT(CT)_4$	56
HK31	$(GT)_6(GA)_{11}$	51

GENOTYPING OF SELECTED MICROSATELLITE LOCI IN TARO

Fluorescent labels were added to successful systems (markers) and PCR amplification was tested with the modified forward primers. Fluorescent labels of each of the eight systems are reported in Table 12. The scoring of alleles was performed using GeneMarker® (Holland and Parson, 2011), and all loci were tested during the initial phase.

Table 12. Labelled primers of successful markers.

Labelled Primers	Optimal Annealing T °C	Company
VIC-Xuqtem84	62°C	Life Technologies (Applied Biosystem)
FAM-Xuqtem88	60°C	Invitrogen
NED-Xuqtem91	56°C	Life Technologies (Applied Biosystem)
PET-Xuqtem110	55°C	Life Technologies (Applied Biosystem)
NED-Xuqtem132	55°C	Life Technologies (Applied Biosystem)
FAM-Xuqtem223	55°C	Invitrogen
VIC-Xuqtem228	60°C	Life Technologies (Applied Biosystem)
PET-HK31	N/A	Life Technologies (Applied Biosystem)

Locus HK31 was selected from Hu et al. (2009) which was found to have the repeat unit $(GT)_6(GA)_{11}$. While the amplification of this locus without a fluorescent label gave single band products, the addition of the fluorochrome PET to its forward primer did not however produce any visible band, and even when PCR conditions were modified, amplification repeatedly failed for this system. Most of the fluorescent labels are bulky, and the addition of a fluorochrome to the forward primer can interfere with the performance of the replication, thus failing amplification of targeted genome regions. This locus was therefore excluded from the analysis.

In Mace and Godwin (2002) Xuqtem132 was reported as a polymorphic microsatellite locus with a complex repetition unit $(TTTGAA)_4$. The forward primer was modified with the addition of the label NED and tested for polymorphism, but this locus was found to be monomorphic in all sample sets (all samples showing the same allele), these results being confirmed by the sequencing of selected samples. Sequencing revealed that the supposed repeat unit published in Mace and Godwin (2002) is not present in the genome region of the sample analysis. This result was also confirmed by the work carried out by Mr Ibrar Ahmed at Massey University in New Zealand on accessions of *C. esculenta* collected in the Asian/Pacific region (Ibrar Ahmed pers. comm.).

PET Xuqtem110 and FAM Xuqtem223 repeatedly showed stutter profiles as shown in Figures 45 and 46 respectively. In order to reduce the false peaks and enable the scoring of genuine alleles, PCR conditions were modified, but because it was not possible to achieve reliable results, these loci were also excluded from the study.

Figure 45. Stutter profile for locus Xuqtem110.

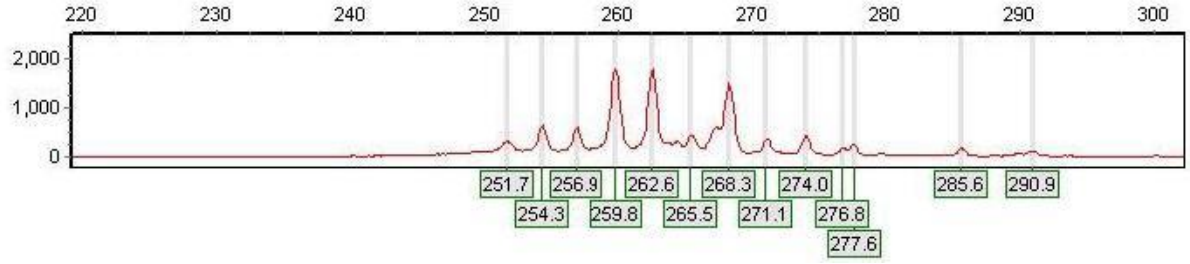
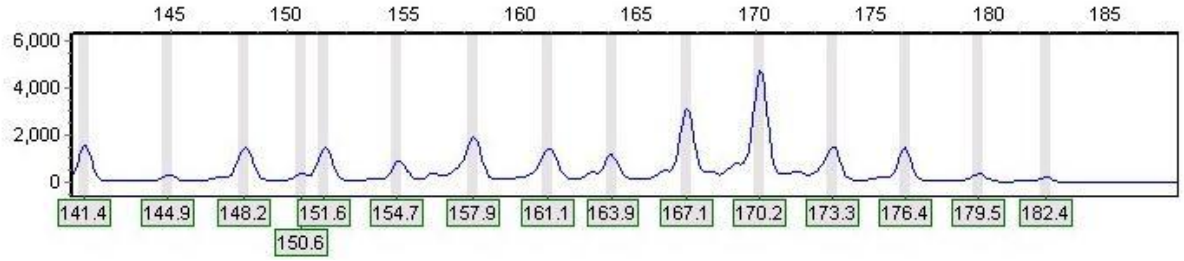


Figure 46. Stutter profile for locus Xuqtem223.



VIC Xuqtem228 was found to be monomorphic in all sample sets, showing one single band 107 base pairs long. In the original publication (Mace and Godwin, 2002), this locus was reported to be monomorphic, showing three allelic forms, with an expected size of 110 base pairs. Due to the calibration of the genotype analyser, measurements of allelic length can slightly vary between laboratories, although it seems odd that a locus can be found in three different forms and yet still be monomorphic. This situation could only be seen if all samples analysed were triploid in nature, showing three different allelic states and showing no variation for the entire sample set. This locus was therefore excluded from the analysis, as it was not seen as useful to the study.

Genotyping of the locus Xuqtem91, with the insertion of the fluorochrome NED, gave a monomorphic profile for 98% of the samples used. However, this locus had been previously investigated at nucleotide level, the sequences of which had been shown to be highly variable. This locus was therefore sequenced in all the sample sets and included in the analysis as

sequences and genotyping data accordingly. The nature of this locus will be discussed in depth in the sequencing section.

FAM Xuqtem88 and VIC Xuqtem84 amplified successfully and proved to be highly informative polymorphic systems. These loci, together with locus Xuqtem91, represent the three molecular markers used in this study and will now be discussed.

The genetic profile of each sample was observed, and in order to achieve consistent results, the approach used in peak scoring was to choose the last identifiable peak as shown in Figure 47 for locus Xuqtem84 and Figure 48 for locus Xuqtem88b.

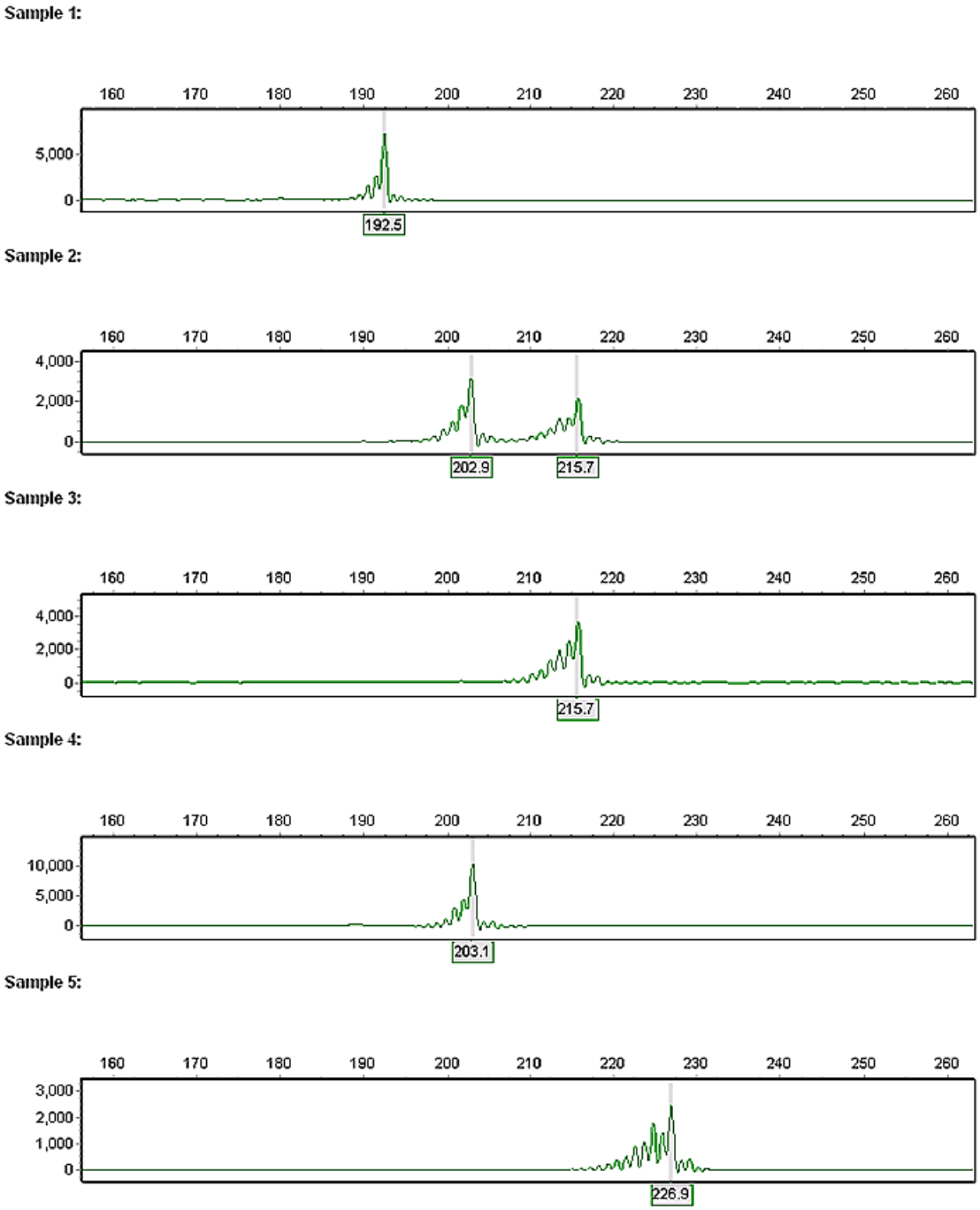


Figure 47. Electropherograms from an ABI310 Genetic Analyser showing, in selected samples, alleles at locus Xuqtem84.

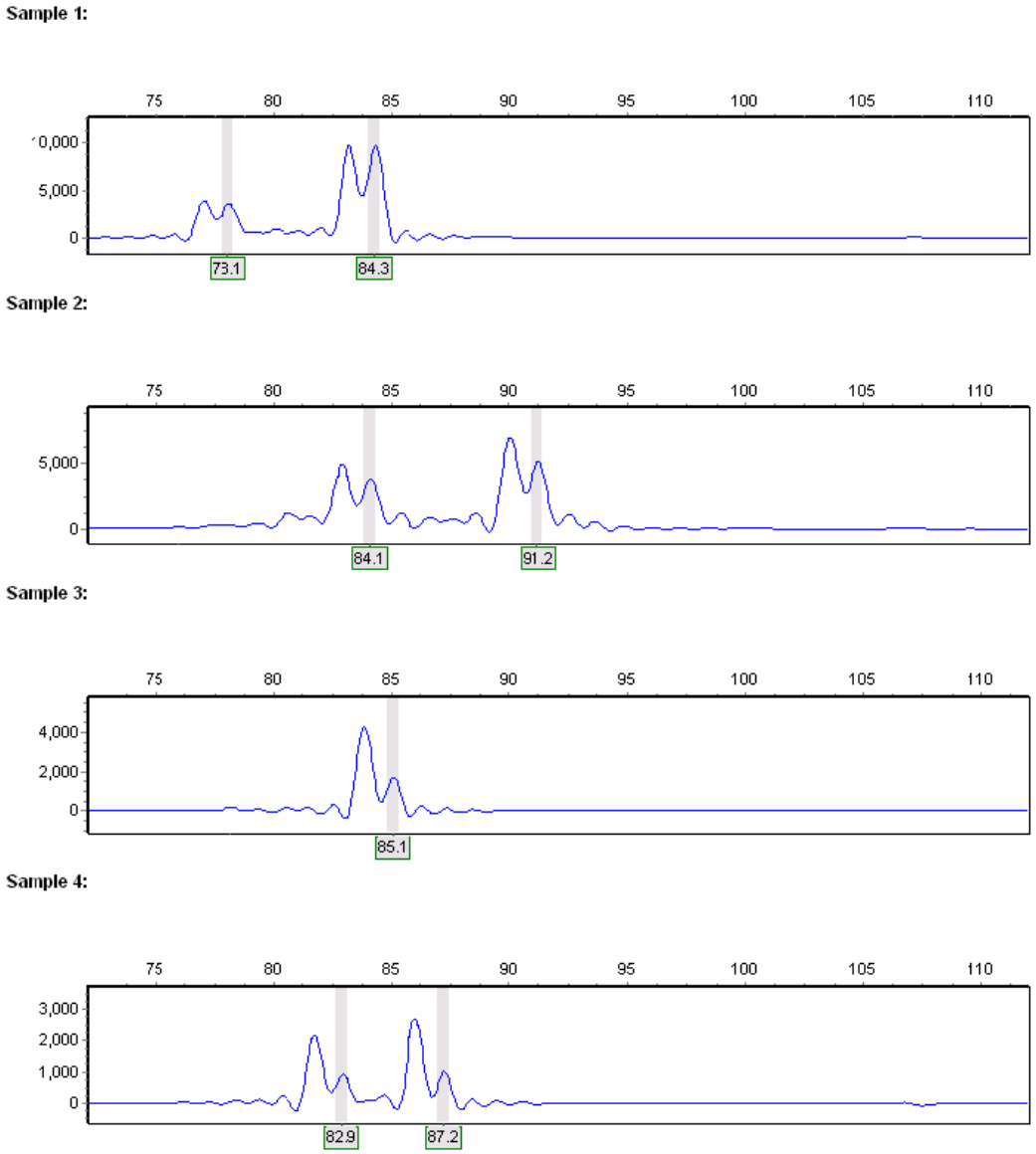


Figure 48. Electropherograms from an ABI310 Genetic Analyser showing, in selected samples, alleles at locus Xuqtem88b.

ON THE POSSIBILITY OF TRIPLOID TARO IN AFRICA

Polyploidy - the occurrence of more than two copies of an entire nuclear genome within a cell - is not uncommon within the genus *Colocasia*. In fact, along with the more common diploid form 2n=2x=28, triploids with 2n=3x=42 are likewise frequently found, especially in the high latitude/high altitude Asian regions (Yen and Wheeler, 1968; Yoshino, 2002; Edison et al., 2003). According to the process from which the triploid form has developed (i.e. autopolyploid or allopolyploid), and the mechanism of allele mutation, triploids can show from one to three different allelic forms at a particular locus. Therefore, by only looking at the allelic pattern it is not always possible to verify the polyploidy nature of a given specimen. In this study, karyotyping analyses targeting the number of chromosomes could not be performed, but sample TG29 which was originally collected in the Philippines and known to be triploid, showed three different alleles both at locus Xuqtem84 and locus Xuqtem88b. Electropherograms of this sample at both loci are shown in Figure 49. Locus Xuqtem88b is a microsatellite locus characterised by the trinucleotide repeat unit $(CAT)_9$. In the electropherogram identified by blue dye colouring, this marker shows peaks at 85, 88 and 91 respectively (Figure 49). Locus Xuqtem84, identified by green dye, is instead characterised by the dinucleotide repeat unit $(CT)_{18}$, in this sample showing alleles at 193, 203 and 216.

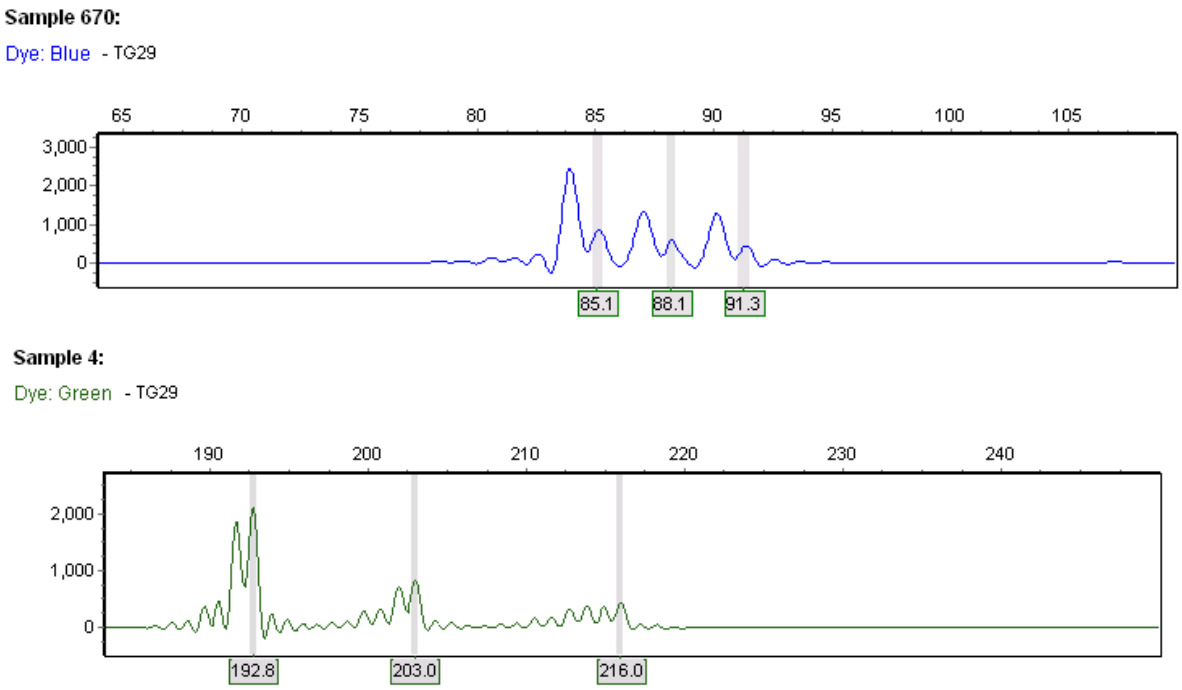


Figure 49. Alleles at locus Xuqtem88b (Blue Dye) and at locus Xuqtem84 (Green Dye) in triploid sample TG29.

At the beginning of this study no genetic analysis whatsoever had been undertaken on taro in Africa, therefore nothing was known about the polyploidy nature and pattern of these plants growing in Africa. In this study, electropherograms of 21 samples of *Colocasia* collected during fieldwork in Africa showed the presence of three peaks at locus Xuqtem88b (allele 81-84-87), suggesting triploids might also be present in Africa. As previously seen, the microsatellite repeat unit at this locus is a trinucleotide composed of (CAT)n, and the alleles found at this locus vary by one or two units, suggesting they evolved under the Stepwise Mutation Model SMM, in which a mutation either increases or decreases the allele value by one unit. This is contrary to the Infinite Allele Model IAM, which assumes an infinite number

of possible alleles at a given locus, so that in the IAM of any new allele arising by mutation is different from those previously present in the species. In Figure 50, electropherograms of two samples with two and three peaks are shown to have this difference in the allelic pattern.

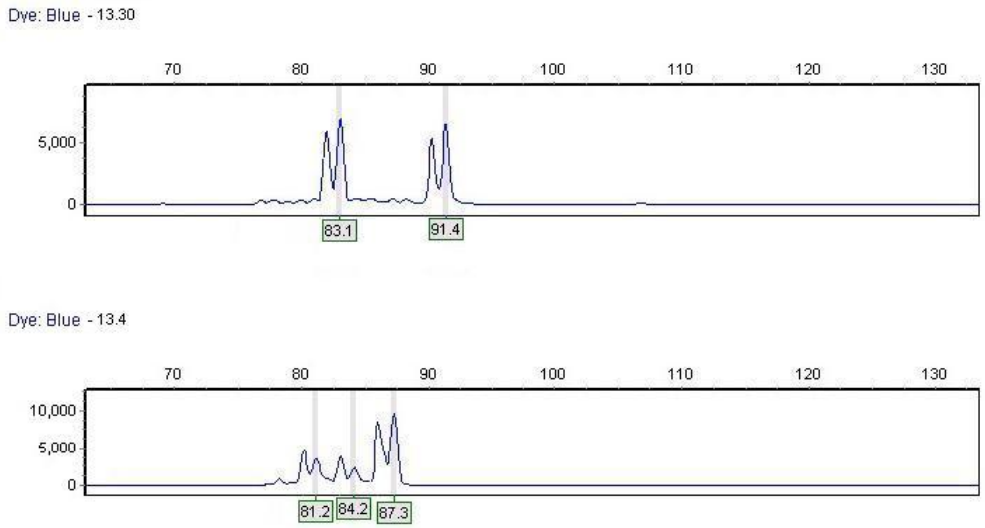


Figure 50. Electropherograms showing two and three alleles at locus Xuqtem88b in two different samples collected in Cameroon.

It is interesting to note that the allelic pattern of these African samples is different from an established triploid from the Philippines (TG29 Figure 49).

Further karyoptyping research aimed at establishing the polyploid nature of dubious triploid samples would therefore be advisable. In Table 13, sample IDs of the supposed triploid samples, the country, the place of collection and its local name are shown. The reader can refer to chapter 4 on the ethnobotanical observations of taro in Africa for more information on this type of plant.

Table 13. Number of samples showing three peaks and place of collection.

Country	Collection site	Sample ID	Local name
Cameroon	Bafang	10.10; 10.22; 10.23; 10.24; 10.25; 10.26	Mangua
Cameroon	Bamenda	12.1; 12.2; 12.3; 12.4; 12.5; 12.6; 12.7; 12.8; 12.9	Mangua
Cameroon	Bambui	13.1; 13.2; 13.3; 13.4; 13.5	Mangua

GENERATION OF DNA SEQUENCING DATA FROM Xuqtem91

Sequencing of 264 base pairs of the microsatellite locus Xuqtem91 was performed on a small set of samples composed of 325 samples of *Colocasia esculenta*. Xuqtem91 is a complex microsatellite locus described in Mace and Godwin (2002) as having a repeat unit consisting of $(TG)_6(GA)_4$. The characterization of this locus as well as others presented in the original paper (Mace and Godwin, 2002) was carried out on a sample of *Colocasia esculenta* originally collected from Fiji, provided by the Secretariat of the Pacific Community (SPC). In their publication, Mace and Godwin (2002) described how they tested the microsatellite loci on thirteen individuals from the Pacific region (Fiji, New Caledonia, Papua New Guinea and Japan) and identified two different alleles for the Xuqtem91 locus of an expected length of 262 base pairs. Subsequently, this marker was also used in the characterization of taro germplasm in the Pacific Islands (Mace et al., 2006; Singh et al., 2008) where it was shown to be present in three allelic forms in the range of 258-262 base pairs.

In our study, the sequencing of this locus produced segments that fall in the allelic range 264-266 with eight different allelic forms which are

reported in Table 14. As previously stated, the genotyping of this locus showed that most of the samples (98%) were of one allele size class, showing single bands which were 264 base pairs in length, and two samples with sequences 266 base pairs long, these being samples TG3 and TG37. Sample TG3 is a specimen of *Colocasia formosana* collected in Taiwan, and being a different species it was excluded from the main analysis. However, as PCR amplification of this locus produced a sequence which was found in its heterozygous form in one sample of *C. esculenta* collected in Japan (ID sample 46.1), it was included in the list of unique alleles. Sample TG37 is a specimen of *Colocasia esculenta* that was collected in a market in Kathmandu, Nepal. This sample is of particular interest because it shows a unique and distinct nucleotide sequence that is widely found as one of the two allelic forms in heterozygous African samples. Interestingly, in this study this allele was not found in samples of Pacific provenance, and whilst a wider sampling of *Colocasia* specimens would be likely to report its presence in other regions, in our sample set it seems to suggest a more frequent geographical occurrence in the Indo-African region.

Unique allelic forms were also found in samples Patt1.1 (collected in state of Kerala, India), T3 (collected in Italy), TG48 (collected in Papua New Guinea), TG19 (collected from Easter Island), 37.1 and 37.2 (both collected in the state of Orissa, India). In the first four samples the microsatellite region is conserved except for a single nucleotide polymorphism A/G in the second

dinucleotide repeat unit. Also, they present two nucleotide substitutions T/G and C/G at the ends of the microsatellite region, as shown in Table 15 and Table 16 in their entire variable region. Conversely, specimens labelled 37.1 and 37.2, originally collected in the state of Orissa in India, show very divergent sequences with six SNPs with the complex repeat unit $(GT)_3CT(GA)_3GT(GA)_2$ and $(GT)_3CTGAGT(GA)_6$ respectively in samples 37.1 and 37.2.

In order to be able to use this locus, and combine it with Xuqtem88b and Xuqtem84 during analysis of population genetics, sequences that identify the highly informative alleles were conventionally translated in arbitrary numbers from 100 to 800 which do not represent numerical values as such, therefore only representing different character states (Table 14).

Table 14. Alleles found at locus Xuqtem91 and categorical value attributed to them.

Sample ID	Microsatellite	Categorical value
T3	G…$(GT)_6(GA)_5$…G	100
T19	T…$(GT)_6GAGG(GA)_3$… C	200
TG48	T…$(GT)_6GAGG(GA)_3$…G	300
Patt1.1	G…$(GT)_6GAGG(GA)_3$…G	400
TG37	G…TATGTAT$(GT)_8$GA…G	500
37.1	G…$(GT)_3CT(GA)_3GT(GA)_2$…	600
37.2	G…$(GT)_3CTGAGT(GA)_6$… G	700
TG3	G…GTTT$(GT)_4(GA)_6$…G	800

It is worth noting that whilst the remaining samples analysed at this locus are 264 base pairs long, sequencing showed that they actually vary in microsatellite unit composition, revealing at times the apparent monomorphic

allelic forms. Table 16 reports the masked heterozygous forms in selected samples.

Table 15. Allelic forms at locus Xuqtem91.

Sample ID	Partial sequence of locus Xuqtem91 showing the microsatellite region	Microsatellite repeat type and SNPs
T3	GGCCCTAGCTGGTCCTACTTTTGTGTGTGTGTGTGTGAGAGAGAGAGCTTGTAGTTGTGTTGTGTTGTGTTCTGTT	G…(GT)$_6$(GA)$_5$…G
TG19	TGCCCTAGCTGGTCCTACTTTTGTGTGTGTGTGTGTGAGGGAGAGAGCTTGTAGTTGTGTTGTGTTCTGTTCTGTT	T…(GT)$_6$GAGG(GA)$_3$… C
TG48	TGCCCTAGCTGGTCCTACTTTTGTGTGTGTGTGTGTGAGGGAGAGAGCTTGTAGTTGTGTTGTGTTGTGTTCTGTT	T…(GT)$_6$GAGG(GA)$_3$…G
Patt1.1	GGCCCTAGCTGGTCCTACTTTTGTGTGTGTGTGTGTGAGGGAGAGAGCTTGTAGTTGTGTTGTGTTGTGTTCTGTT	G…(GT)$_6$GAGG(GA)$_3$…G
TG37	GGCCCTAGTTGGTCCTACTTTTATGTATGTGTGTGTGTGTGTGTGAGCTTGTAGTTGTGGTGTTGTGTTCTGTT	G…TATGTAT(GT)$_8$GA…G
37.1	GGCCCTAGCTGGTCCTACTTTTGTGTGTCTGAGTGAGAGAGTGAGAGCTTGTATTTGTGTTGTGTTGTGTTCTGTT	G…(GT)$_3$CT(GA)$_3$GT(GA)$_{2...}$
37.2	GGCCCTAGCTGGTCCTACTTTTGTGTGTCTGAGTGAGAGAGAGAGAGCTTGTATTTGTGTTGTGTTGTGTTCTGTT	G…(GT)$_3$CTGAGT(GA)$_{6...}$ G
TG3	GGCCCTAGCTGGTCCTACTTTTGTTTGTGTGTGTGAGAGAGAGAGAGCTTGTAGTTGTGTTGTGTTGTGTTCTG	G…GTTT(GT)$_4$(GA)$_6$…G

Table 16. Heretozygous forms at locus Xuqtem91.

Sample ID (examples)	Partial masked heterozygous sequence	Microsatellite repeat type and SNPs
1.1	K[3]GCCCTAGCTGGTCCTACTTTTGTGTGTGTGTGTGAGRAGAGAGCTTGTAGTTGTGTTGTGTTGTGTTCTGTT	G...(GT)$_6$(GA)$_5$…G T...(GT)$_6$GAGG(GA)$_3$…G
TG4	KGCCCTAGCTGGTCCTACTTTTGTGTGTGTGTGTGAGGGAGAGAGCTTGTAGTTGTGTTGTGTTSTGTTCTGTT	G…(GT)$_6$GAGG(GA)$_3$...G T…(GT)$_6$GAGG(GA)$_3$...C
2.1	KGCCCTAGCTGGTCCTACTTTTGTGTGTGTGTGTGAGGGAGAGAGCTTGTAGTTGTGTTGTGTTGTGTTCTGTT	T…(GT)$_6$GAGG(GA)$_3$...G G…(GT)$_6$GAGG(GA)$_3$...G
TG26	TGCCCTAGCTGGTCCTACTTTTGTGTGTGTGTGTGAGGGAGAGAGCTTGTAGTTGTGTTGTGTTSTGTTCTGTT	T…(GT)$_6$GAGG(GA)$_3$…G T…(GT)$_6$GAGG(GA)$_3$…C

[3]IUPAC convention for nucleic acid code: K= G/T; R= Purine (G/A); S=C/T.

GENETIC VARIATION OF TARO IN AFRICA

In order to study the genetic variation in accessions of taro collected in Africa and outside Africa, populations were first defined. Generally speaking, a population is a local group of individuals that are able to interbreed. However, the geographic delimitation of any population is not always straightforward, especially when sampling has not been conducted consistently in all regions surveyed. In this study the geographical sampling scale and the historical background on which this research rests were considered, with a total number of 12 populations being defined. In some cases, populations were defined on a country basis, while in others several countries were grouped together. The choice of not grouping together populations with a low number of samples was considered on the basis of the historical as well as the geographical background. Conversely, where appropriate, wider regions were characterised so that comparison between continents could be performed.

Of the 693 original samples, the 20 dubious triploid ones were deleted from the sample set. Moreover, samples with missing data in more than one locus were also avoided. The resulting 660 samples therefore represent the core dataset used in this study. Table 16 shows the populations and the regions characterised, the countries included in each population and the number of samples in each of them.

Table 17. Populations and regions identified in this study.

Population	Country	Region	N. of samples
1. West Congo	Democratic Republic of Congo	West Africa	39
2. Cameroon	Cameroon	West Africa	176
3. Kenya	Kenya	East Africa	114
4. Tanzania	Tanzania	East Africa	126
5. Nigeria	Nigeria	West Africa	35
6. Central Africa	Democratic Republic of Congo, Burundi, Uganda	Central Africa	85
7. Ethiopia	Ethiopia	East Africa	6
8. Mediterranean	Italy, Egypt, Cyprus	Mediterranean	5
9. Madagascar	Madagascar, La Réunion	East Africa	8
10. India	India, Sri Lanka	India	26
11. Pacific Region	Society Islands, Papua New Guinea, Easter Island, Philippines, Australia	Japan	28
12. Japan	Japan	Pacific	12
Total			660

GENETIC DIVERSITY OF TARO IN AFRICA

The genetic diversity of 660 samples of taro collected in Africa and elsewhere was analysed using three SSR polymorphic markers. Genetic diversity can be present at any particular locus within an individual, at population level and within the entire group analysed. The quantification of the level of polymorphism within the whole group was calculated through the following parameters: the number of alleles, allele range, Polymorphism Information Content PIC, Expected Heterozygosity (He), and Observed Heterozygosity (Ho). These values are reported in Table 17.

Table 18. Genetic diversity in the collection of *Colocasia esculenta* in Africa and elsewhere.

Marker	Sample	No of obs.	Genotype	Allele	Expected	Observed	PIC
Xuqtem84	660	634	30	22	0.632	0.267	0.601
Xuqtem88b	660	660	26	14	0.856	0.785	0.841
Xuqtem91	660	552	13	8	0.730	0.897	0.692
Mean	660	615	23.3	15	0.739	0.649	0.711

The number of genotypes varied from 13 to 30 with an average of 23.3. The number of alleles per primer ranged from 8 to 22, with an average of 15. The polymorphism information content (PIC), a measure introduced by Botstein et al. (1980) to describe the measure of informativeness of a genetic marker, ranged from 0.601 to 0.841, with an average of 0.711, showing the nuclear microsatellites to be highly informative. The expected heterozygosity (He) varied from 0.632 to 0.856, with an average of 0.739. The observed heterozygosity (Ho) instead varied from 0.267 to 0.897, with an average of

0.649. These values do vary significantly in the mean, and at locus Xuqtem88b and Xutem91, however, the discrepancy between He and Ho in Xuqtem84 may indicate the presence of null alleles (alleles that cannot be detected due to a mutation in the primer regions), which decrease the observed heterozygosity.

ALLELIC PATTERN ACROSS POPULATIONS

The graph in Figure 51 represents the allelic pattern across the populations analysed. Bar plots indicate the number of alleles (Na), number of effective alleles (Ne)= 1/(sum pi^2), number of private alleles (No) and the expected heterozygosity (He) across the populations indicated by the red curve. This latter drops rapidly in population 7 (Ethiopia), population 8 (Mediterranean), and population 9 (Madagascar), as a consequence of the limited sampling carried out in these regions. For this reason the allele frequencies in these populations should be taken as a rough indication of their genetic diversity and not necessarily as robust values.

It is also possible to see that the Indian group is the population which shows the highest number of alleles, the highest number of private alleles (alleles present only in one population) and consequently the highest He. This is followed by the Pacific population. This pattern confirms that the highest

diversity of taro is found in the Asian region, the suggested geographic of origin of taro.

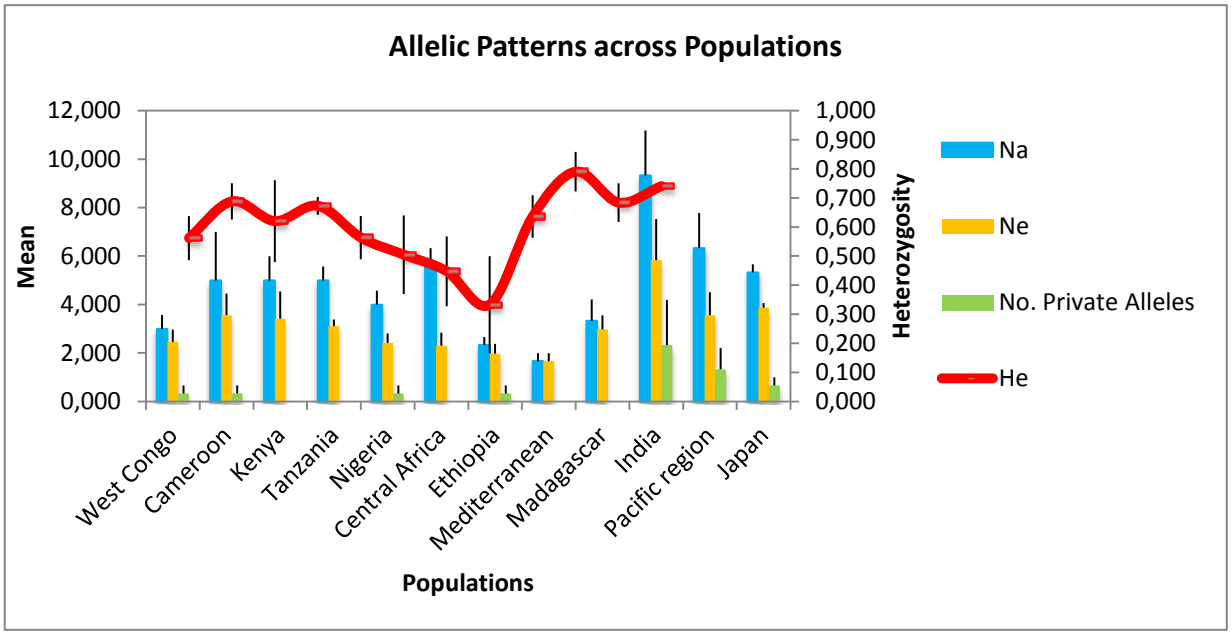


Figure 51. Allelic patterns across taro populations.

MICROSATELLITE LOCUS XUQTEM84

The nuclear microsatellite locus Xuqtem84 was described in Mace and Godwin (2002) as having a dinucleotide repeat unit $(CT)_{18}$ and showing seven allelic forms. In the sample set analysed, this marker was found to be very informative, showing 22 allelic forms. In Figure 48 some of the alleles found at this locus have been shown, and the distribution of the alleles in each population is reported in Figure 52 and Figure 53. Within this locus, alleles 193, 203, 216 and 218 are the most frequent alternative variant forms.

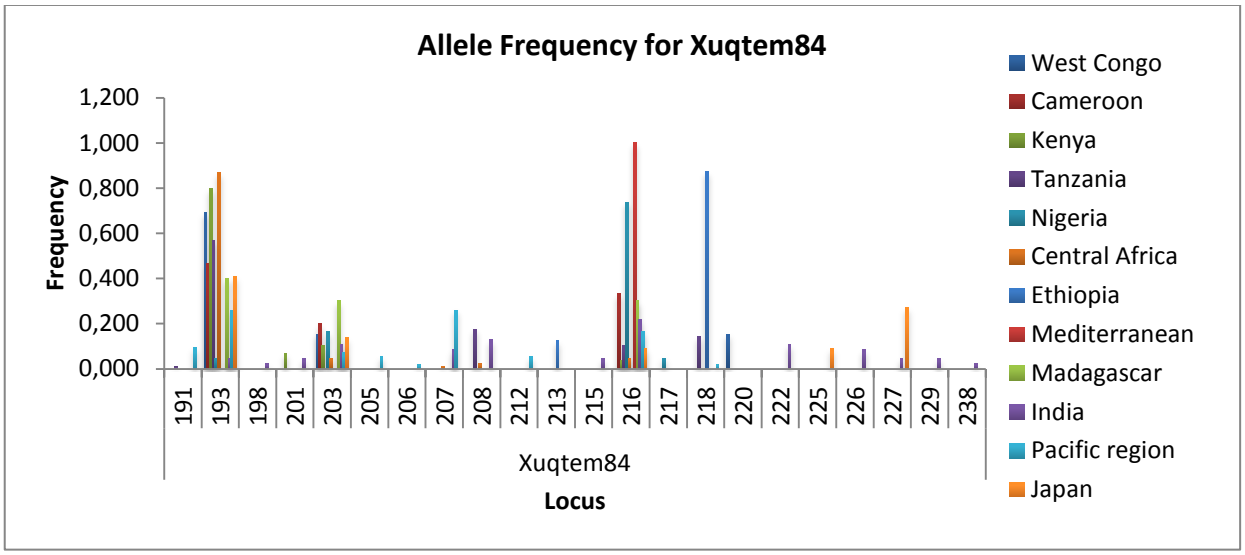


Figure 52. Allele frequency at Locus Xuqtem84.

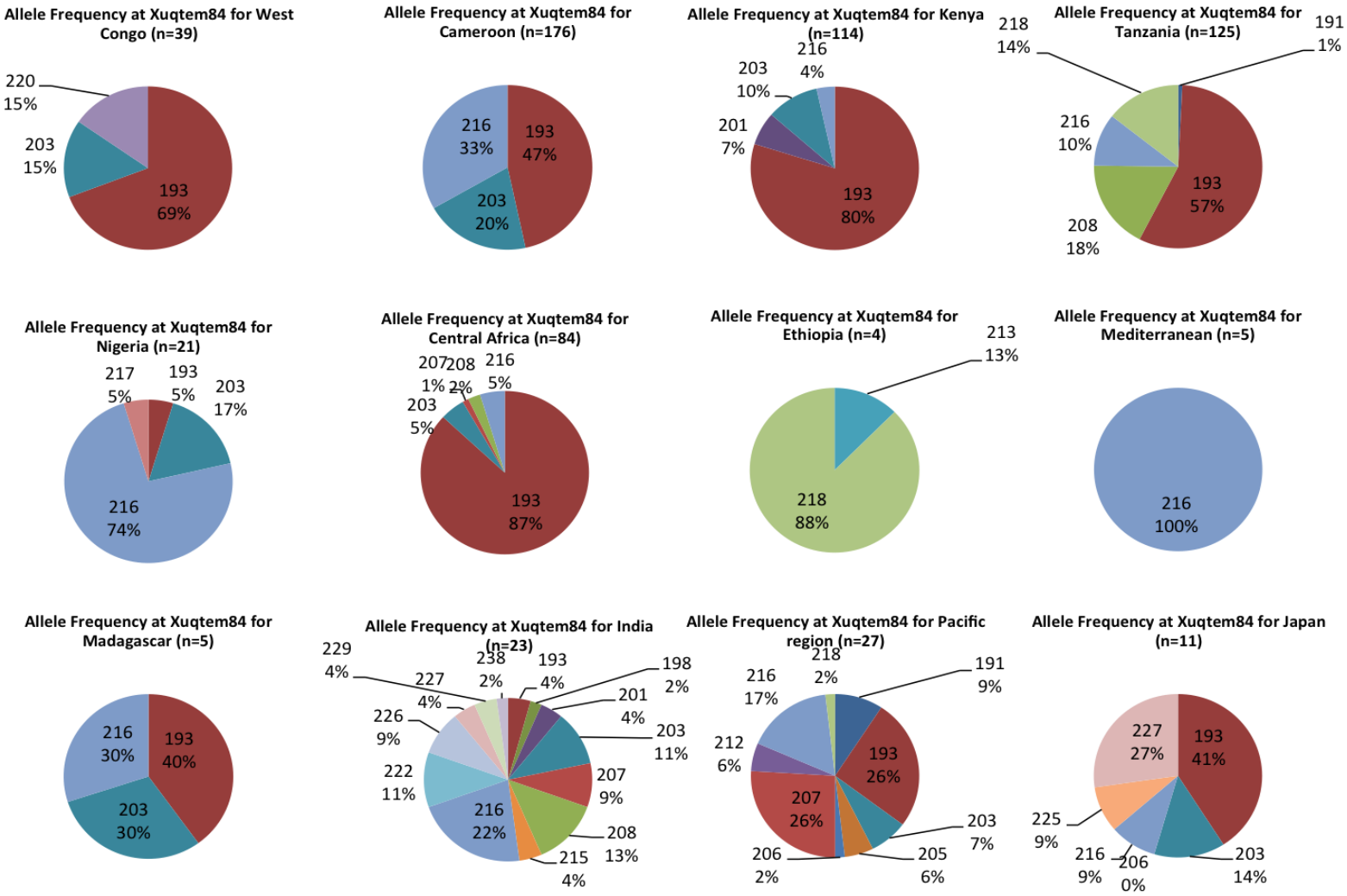


Figure 53. Allele frequency at locus Xuqtem84 in each population.

MICROSATELLITE LOCUS XUQTEM88B

Locus Xuqtem88b is a microsatellite that was described by Mace and Godwin (2002) as having a trinucleotide repeat unit $(CAT)_9$. This marker was also found to be very informative, showing 14 allelic forms and an expected heterozygosity value of 0.785. In Figure 49 at pag 141 some of the alleles found at this locus have been shown, and the distribution of the alleles in each population is reported in Figure 54 and Figure 56.

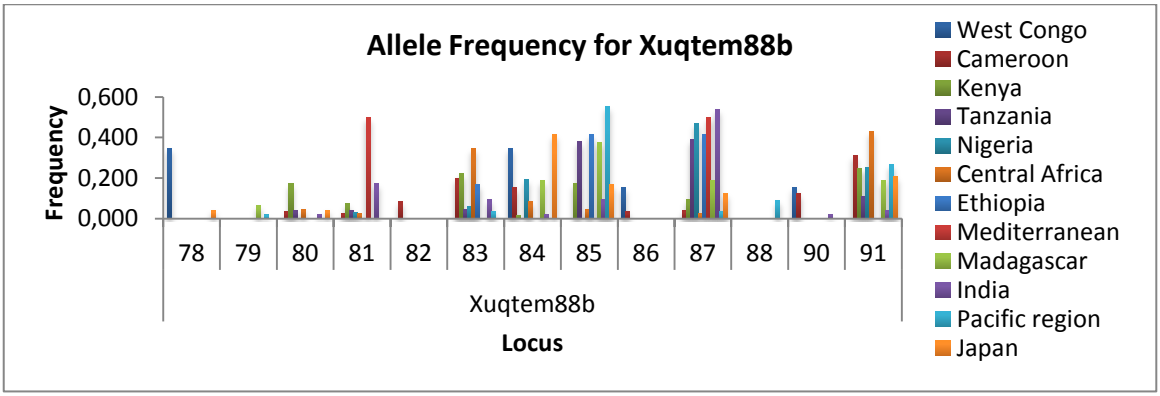


Figure 54. Allele frequencies at Locus Xuqtem88b.

However, sequencing of this locus revealed the presence of other repeat units in the flanking regions, and more specifically in Figure 55 it is possible to observe other sites that can cause length variation such as a dinucleotide $(CT)_4$, and three single nucleotide repeats as shown by $(G)_4$, $(C)_4$ and $(T)_5$. These units are likely to decrease or increase as a consequence of the polymerase slippage during replication, so that the polymorphism associated with this locus is not likely to be completely left to the (CAT)n unit, but also to the other repeat units.

This issue has to be taken into consideration when assuming a Stepwise Mutation Model for the evolution microsatellite. In fact, the addition or decrease of a single nucleotide results in fragments that do not differ by one or more trinucleotide unit.

Forward primer

CACACATACCCACATACACGGGGCTTGGCCCCCTCTCTCTTAATCATTTTTGTGATCATCATCATCATCATCATCATTAGAGCCTGG

Reverse Primer

Figure 55. Sequence of locus Xuqtem88b in which the repeat units (G)4, (C)4, (CT)4, (T)5, and the repeat unit (CAT)7 are shown respectively in purple, green, blue, orange and red.

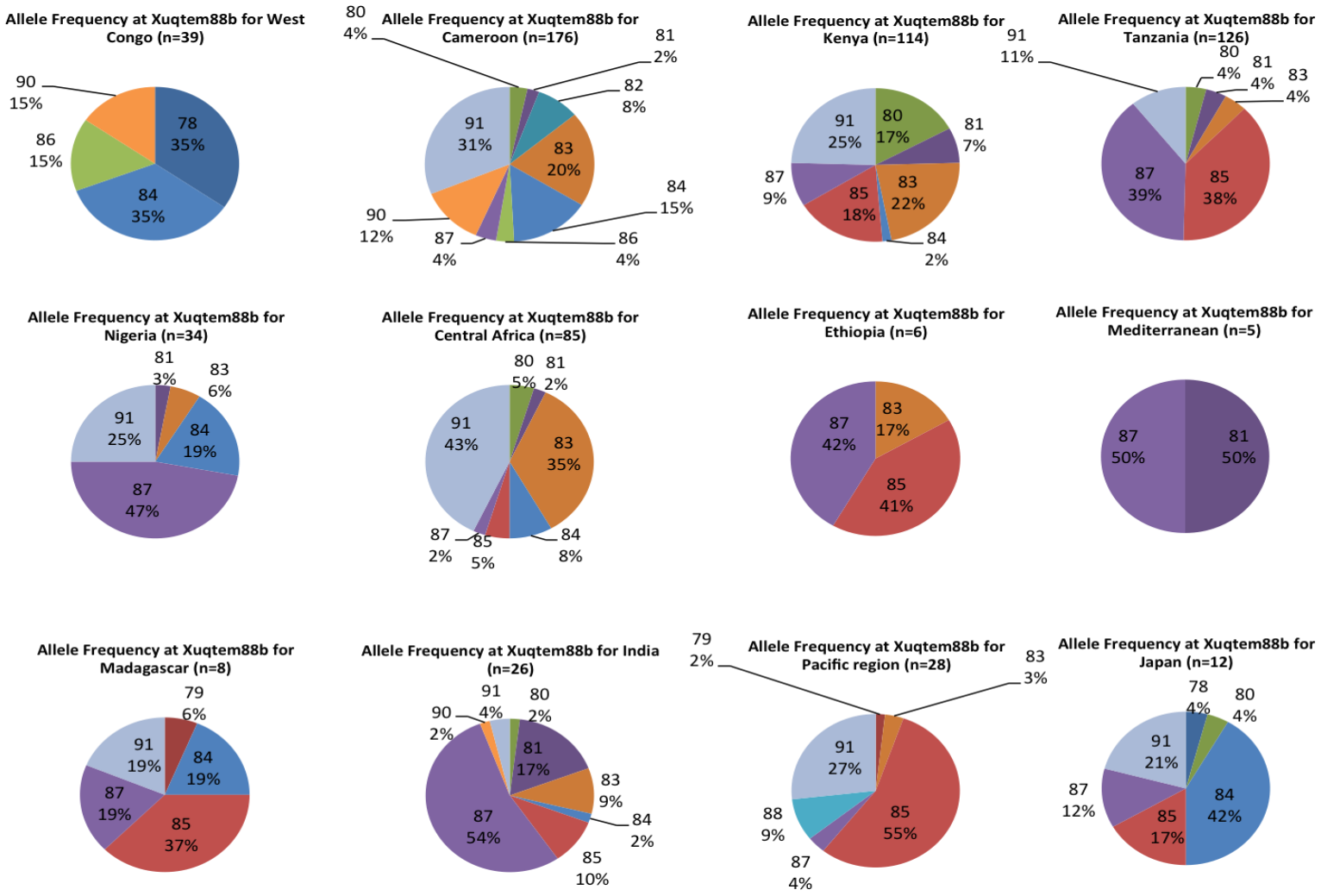


Figure 56. Allele frequency at locus Xuqtem88b in each population.

MICROSATELLITE LOCUS XUQTEM91

Locus Xuqtem91 is a microsatellite which was described (Mace and Godwin, 2002) as having a di-dinucleotide repeat unit $(TG)_6(GA)_4$ and as being present in two allelic forms. However, the sequencing of this locus showed that the supposed repeat unit is $(GT)_n(GA)_n$ and within the sample set analysed it showed eight gene forms, proving to be highly variable and informative (Table 15 and Table 16 pag 149). The allele frequency at this locus is shown in Figure 57 and Figure 58.

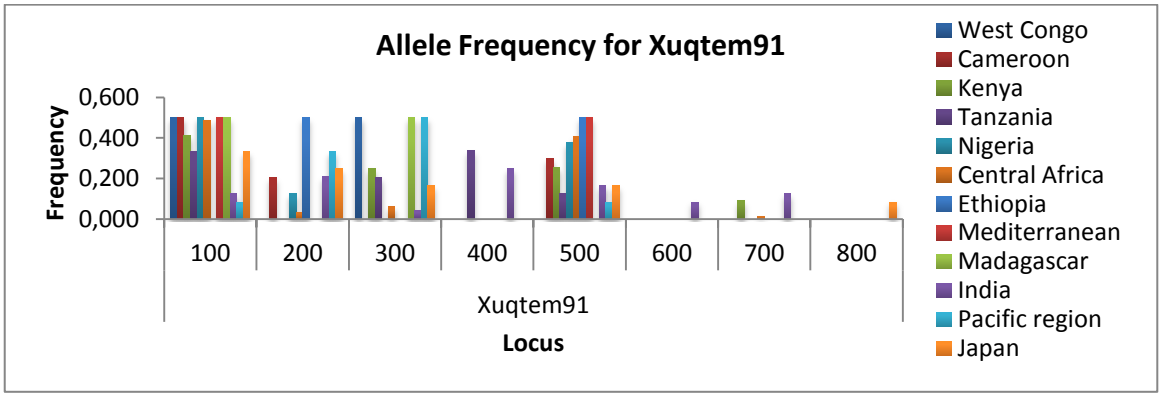


Figure 57. Allele frequencies at locus Xuqtem91.

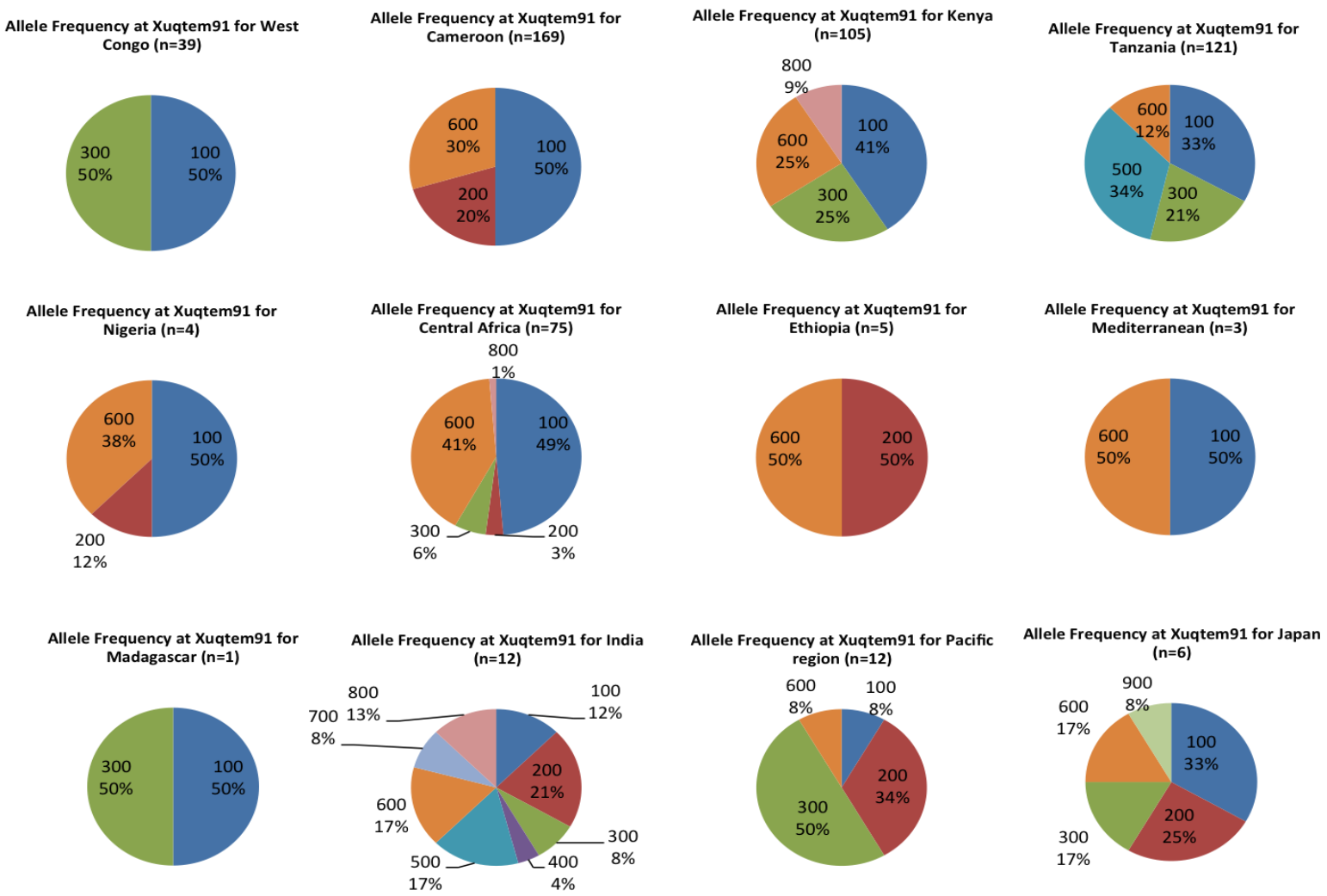


Figure 58. Allele frequency at locus Xuqtem91 in each population.

AMOVA ANALYSIS ON TARO POPULATION IN AFRICA

In order to quantify the genetic diversity between groups, a statistical approach was used, and Analysis of Molecular Variance AMOVA was performed with GenAlEx (Peakall and Smouse, 2012). This type of analysis is equivalent to the Analysis of Variance ANOVA, except that it does not require the assumption of a normal distribution, with molecular data being used instead. Figure 59 shows the representation of the genetic structure within and among populations.

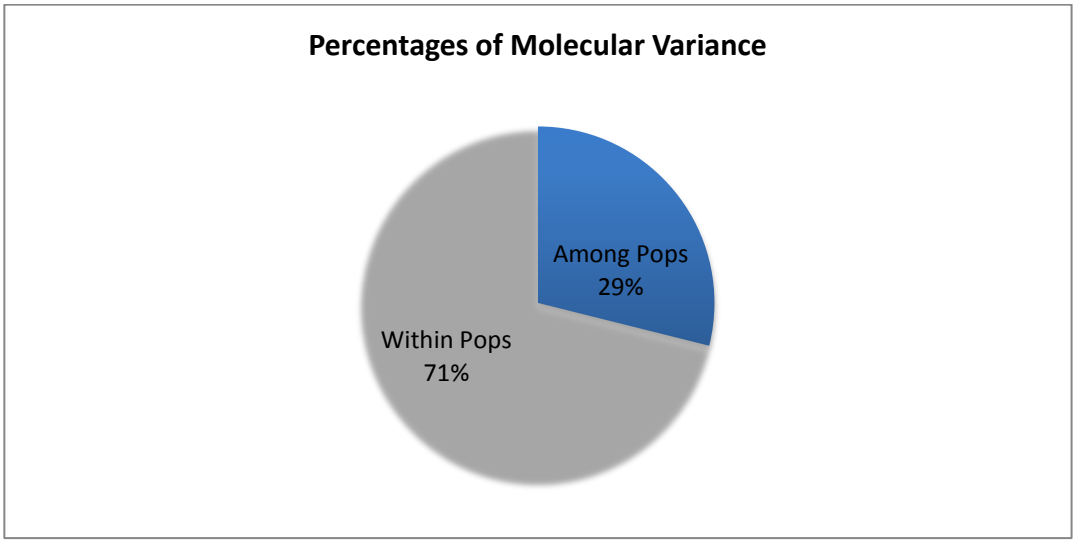


Figure 59. Statistical analysis AMOVA performed on taro populations in Africa and elsewhere.

The within-population variation accounted for most variation, indicating a mixed assortment of the genetic variation in all populations. Taking this comparison into account, the variation is limited to 29%.

PRINCIPAL COORDINATES ANALYSIS PERFORMED ON TARO SAMPLES

When dealing with multivariate data (e.g. data that show many variables), it is useful to reduce the number of variables to just a few to uncover the relationship that exists between all samples. Multivariate analysis aims to find these relationships. To this end, Principal Coordinates Analysis PCoA was performed with the software GenAlEx 6.5 (Peakall and Smouse, 2012). By constructing a dissimilarities matrix and using an appropriate genetic distance, this computational analysis has the capability to represent in a two dimensional graphic the principal coordinates in which the entire variability can be summarised. In order to analyse the microsatellite data, Gower distance was the genetic distance used to calculate the dissimilarity matrix (Gower, 1966). Figure 60 shows the results of the analysis of the first principal coordinates. Each sample is identified by a symbol that shows the original population, as indicated in the legend. When two clones that belong to different populations are plotted on the same spot, the labels overlap.

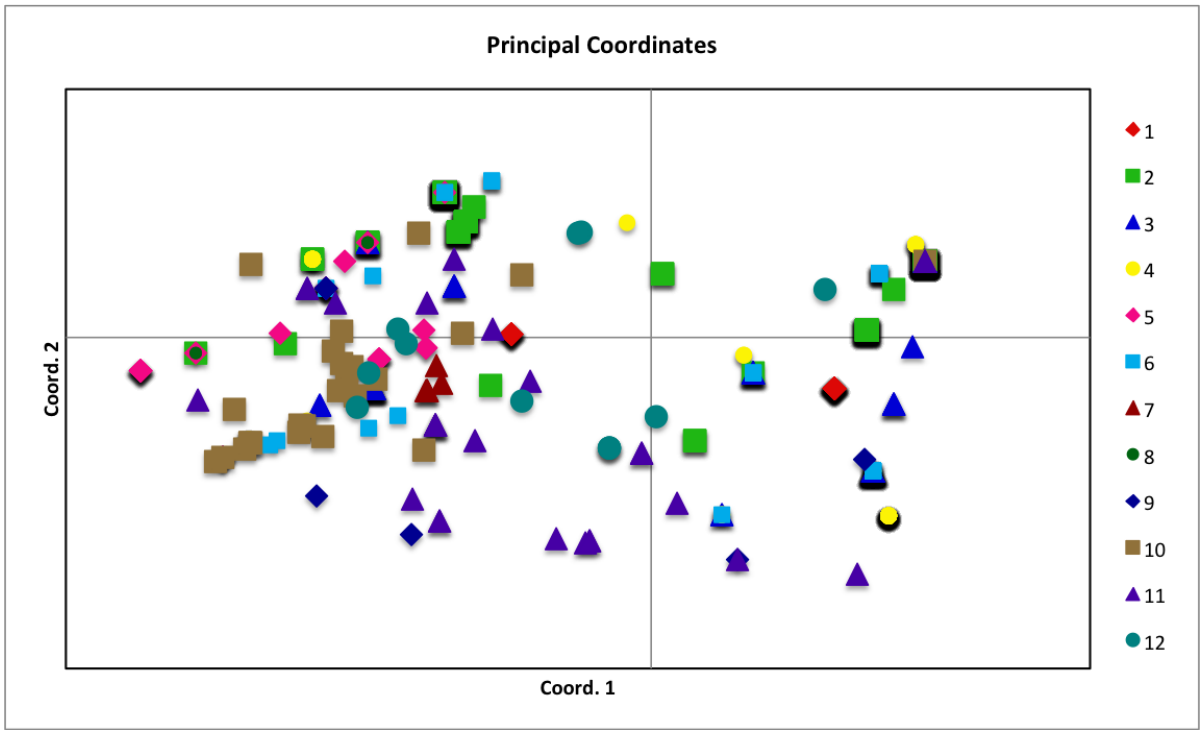


Figure 60. Principal coordinates analysis performed with GenAlEX based on all microsatellite data.

Table 18 shows values for the first 10 axes. The first coordinate or eigenvalue is 15.239 accounting for about the 30% of the diversity (29.398%), the second coordinate or eigenvalue is 10.213 accounting for almost the 20% of the variability (19.703%), until the 10th axis is reached after which the percentage is found to be under 0.25%.

Table 19. Eigenvalues and percentage for each of the 10 axes.

Axis	1	2	3	4	5	6	7	8	9	10
Eigenvalue	15.239	10.213	3.7442	2.9676	2.4824	1.0868	0.69608	0.57373	0.43788	0.3314
Percentage	29.398	19.703	7.2234	5.7251	4.7891	2.0966	1.3429	1.1068	0.84475	0.63934

A similar analysis was done using PAST (Hammer et al., 2001). Even though the appearance of the plot obtained differs slightly, it still depicts two main clusters, which are more distinct using this software. When each sample

is coloured according to their chloroplast type GP or RR, the two groups are visibly separated. It is important to stress that the actual chloroplast type information is not employed in the analysis and that the result is completely independent from the chloroplast identification. In Figure 61 the red dots identify samples of taro characterised by the chloroplast RR type, the green dots corresponding to the GP with the black dots being samples with no chloroplast information. The PCoA therefore reveals a clustering of taro plants based on the chloroplast type. Taro is a clonally propagating plant, but the few mixed dots in each group could represent breeding events between two different types of plants, the GP type and the RR type.

In order to investigate more within each of the two main groups, a 3D plot was produced using the Landmarks 3D application in PAST, and due to its capacity of being able to reproduce animations it was possible to select a later view from the left hand side. Figure 62 shows a lateral view of the plot drawn in Figure 61.

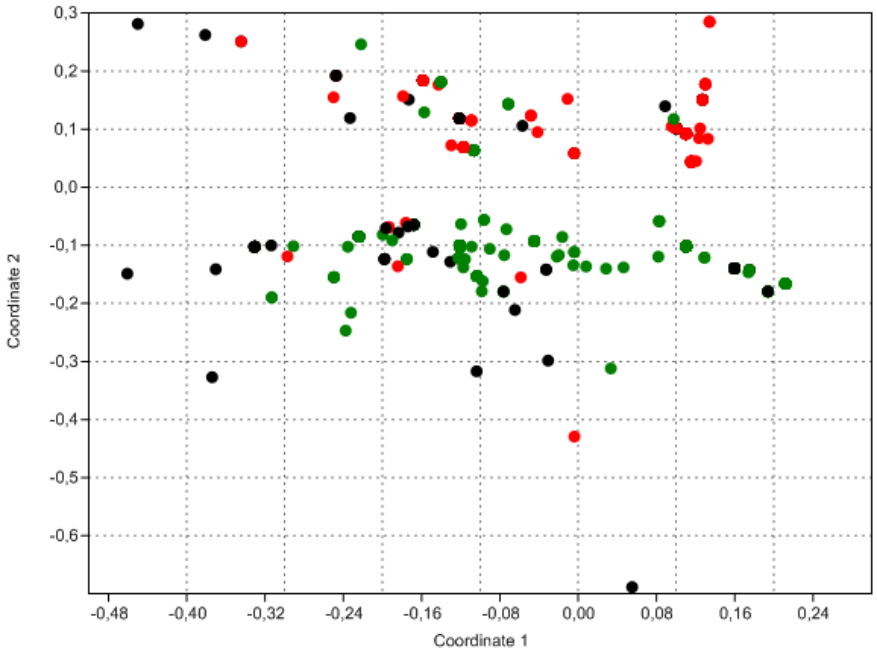


Figure 61. PCoA plot performed with PAST. Samples were coloured according to their chloroplast type, green for GP chloroplast morphotype, red for RR chloroplast morphotype, and black when the chloroplast information was missing.

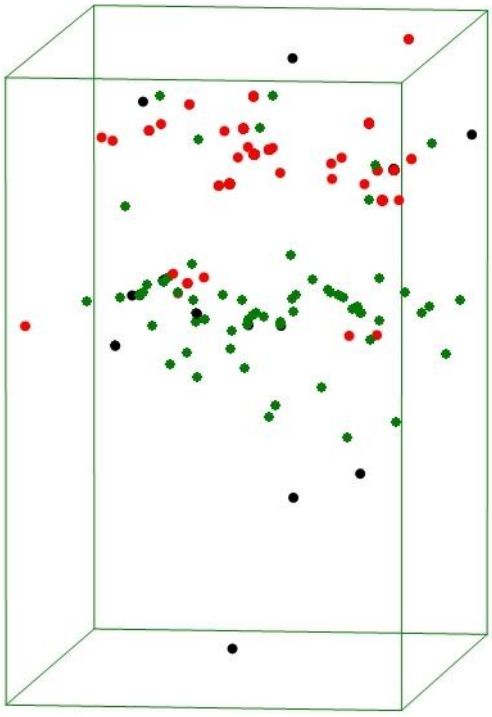


Figure 62. Lateral view of the PCoA 3D plot.

The third component visible in the 3D plot does not resolve the structure in taro samples. However, the use of a higher number of molecular markers could help the identification of a substructure within the species.

CLUSTER ANALYSIS PERFORMED ON TARO SAMPLES IN AFRICA AND ASIA

Another method to identify the underlying structure of the data is to perform a cluster analysis in which samples are associated according to their similarity. The cluster analysis was performed with PAST (Hammer et al., 2001). Data were first converted into a binary matrix, and then a genetic distance matrix between accessions was constructed with Jaccard coefficient distance (1908), from which a UPGMA (Unweighted Pair Group Method with Arithmetic Mean) dendrogram was derived.

The UPGMA clustering analyses at the cophenetic correlation value of 0.941 grouped the 660 accessions into two super clusters. A bootstrap value of 100 confirmed the separation of the two groups. All the other branches had values under a significance threshold so that the sub-groups could not be ruled out. It would seem that bootstrap values tend to get smaller in large datasets (Sanderson, 1989); this is probably because in order for a cluster or clade to be counted as "supported" in a bootstrap replicate, it has to contain exactly the same set of terminal nodes (taxa) in the original as in the replicate. As the number of taxa in a clade is increased, it is more likely that a single taxon will drop out in the replicate, such that the bootstrap support reduces. This is one of several reasons why bootstrapping in systematics is somewhat questionable.

Figure 63 represents the UPGMA dendrogram constructed using the Jaccard matrix. The dendrogram obtained shows two main superclusters, namely supercluster 1 and supercluster 2. Even though this kind of analysis does not provide information for reconstructing phylogenetic relationships, the 100% confidence bootstrap value between the two superclusters suggests that these groups represent two different types of taro plant.

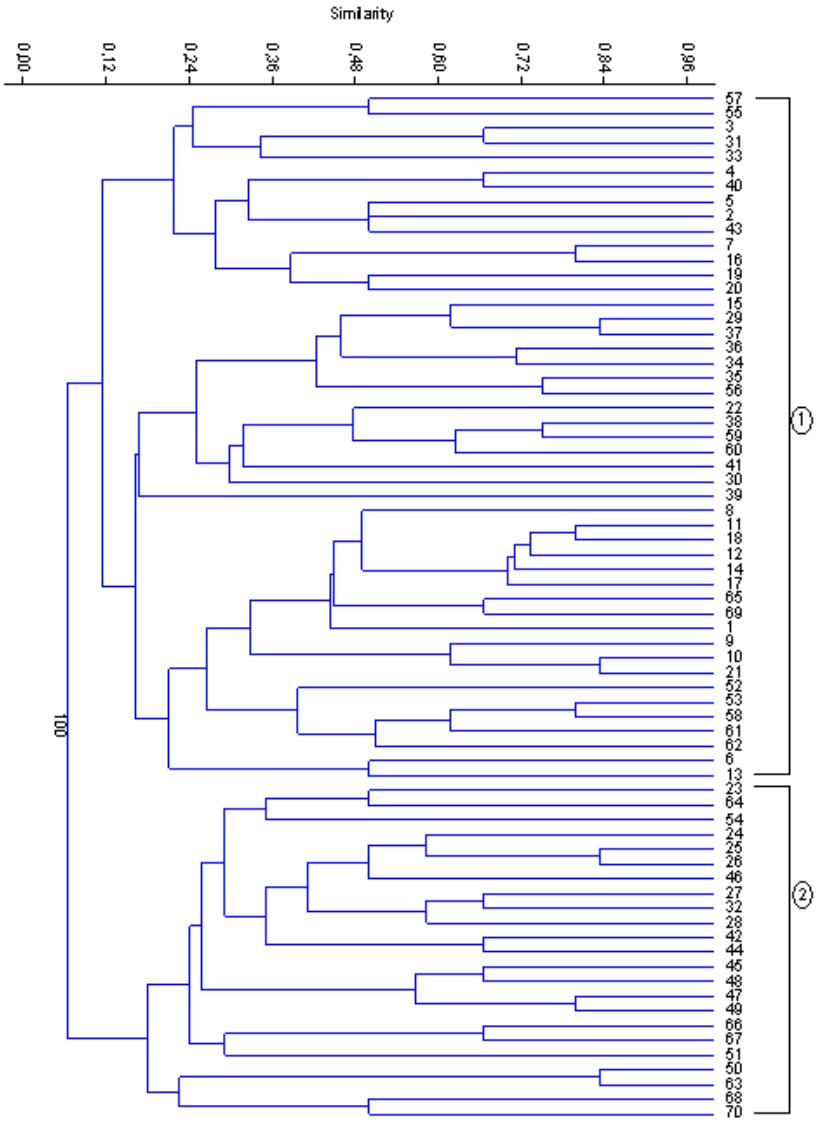


Figure 63. UPGMA dendrogram of the genotypes.

STRUCTURE ANALYSIS ON AFRICAN TARO POPULATIONS

In order to compare the results of the cluster analysis, STRUCTURE (Pritchard et al., 2000) was employed to test the most probable number of groups within taro samples. STRUCTURE uses a Bayesian approach in which population structure is inferred and individuals are assigned to populations. This software has limitations in dealing with samples that are distributed over a wide area; therefore only African taro samples were used. In order to identify the most likely number of populations (K), the admixture model was used with a burn-in period of 10,000 Markov Chain Monte Carlo iterations and 100,000 run length. The number of clusters (K) was tested from 1 to 20 and each run was repeated 10 times to ensure the STRUCTURE was consistent across runs and values of K. In order to choose the optimal value of K, LnP(D)=L(K) was obtained with STRUCTURE HARVESTER (Earl and von Holdt, 2012). The results obtained from the analyses performed are shown in Figures 64 to 68. When K is approaching a true value, L(K) reaches a plateau or increases slightly showing increasing high variance between runs (Pritchard and Wen, 2003). Figure 64 shows an optimal value of K=4 for taro populations in Africa, after which K reaches a stable level and the standard deviation increases.

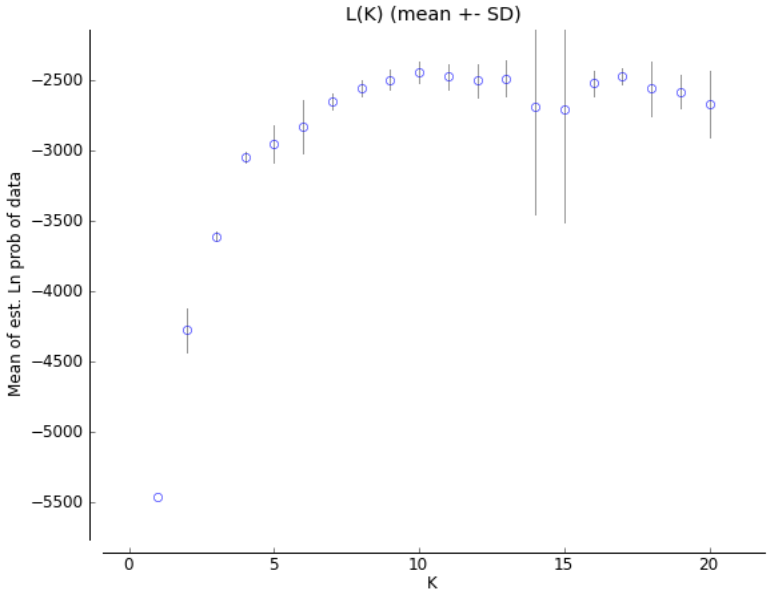


Figure 64. Plot of mean likelihood L(K) and variance per K value.

In order to test for K=4, the Evanno method (Evanno e al., 2005) was employed and ΔK calculated (Earl and vonHoldt, 2012). Figure 65 shows that ΔK=4 as calculated with STRUCTURE, suggesting the presence of four populations of taro in Africa.

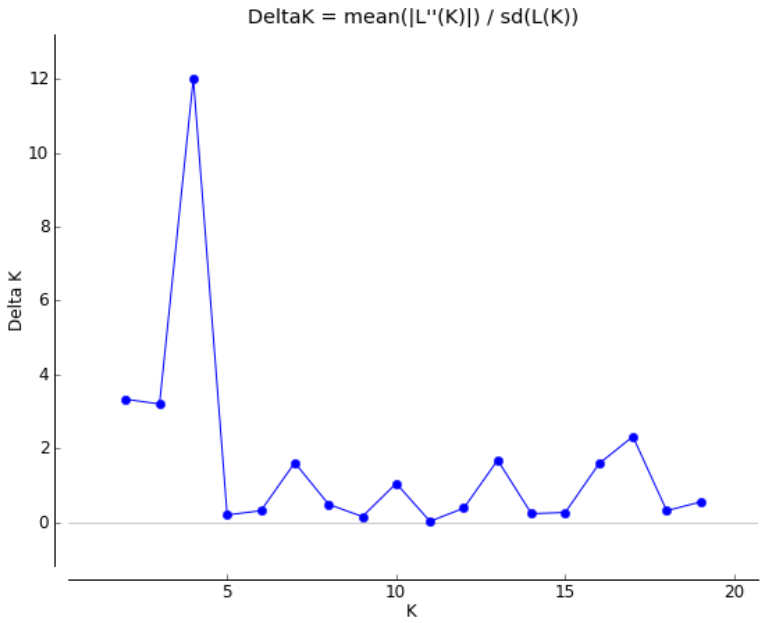


Figure 65. ΔK calculated with the Evanno method.

In order to visualise the proportion of the ancestry of each individual inferred from each cluster, and to understand how this relates to the previously defined populations, STRUCTURE produces a bar plot in which each bar represents an individual which is coloured according to the proportion of each allele found in each of the K populations. Figure 66 shows this proportion for each of the 660 samples of taro in Africa. Interestingly, the bar-plot highlights the clonal nature of taro. In fact, most of the samples seem to belong to a single population and less frequently share part of their make-up with more than one.

When the four populations (K) identified by STRUCTURE are plotted on a map (Figure 67), a genetic assortment is evident in each country with the exclusion of the Mediterranean area that are seen to be homogenous. Generally, there seems to be a correlation between clusters identified by

STRUCTURE and the GP and RR chloroplast genotypes. Blue coloured groups are defined by the chloroplast RR genotype in 100% of the samples analysed. Meanwhile, samples that fall into the green group are all of the GP type. The yellow group is of the RR type in 70% of the samples and GP in the remaining 30%. Finally, the red group is of the GP type in 91% of the samples and the remaining 9% is of the RR type.

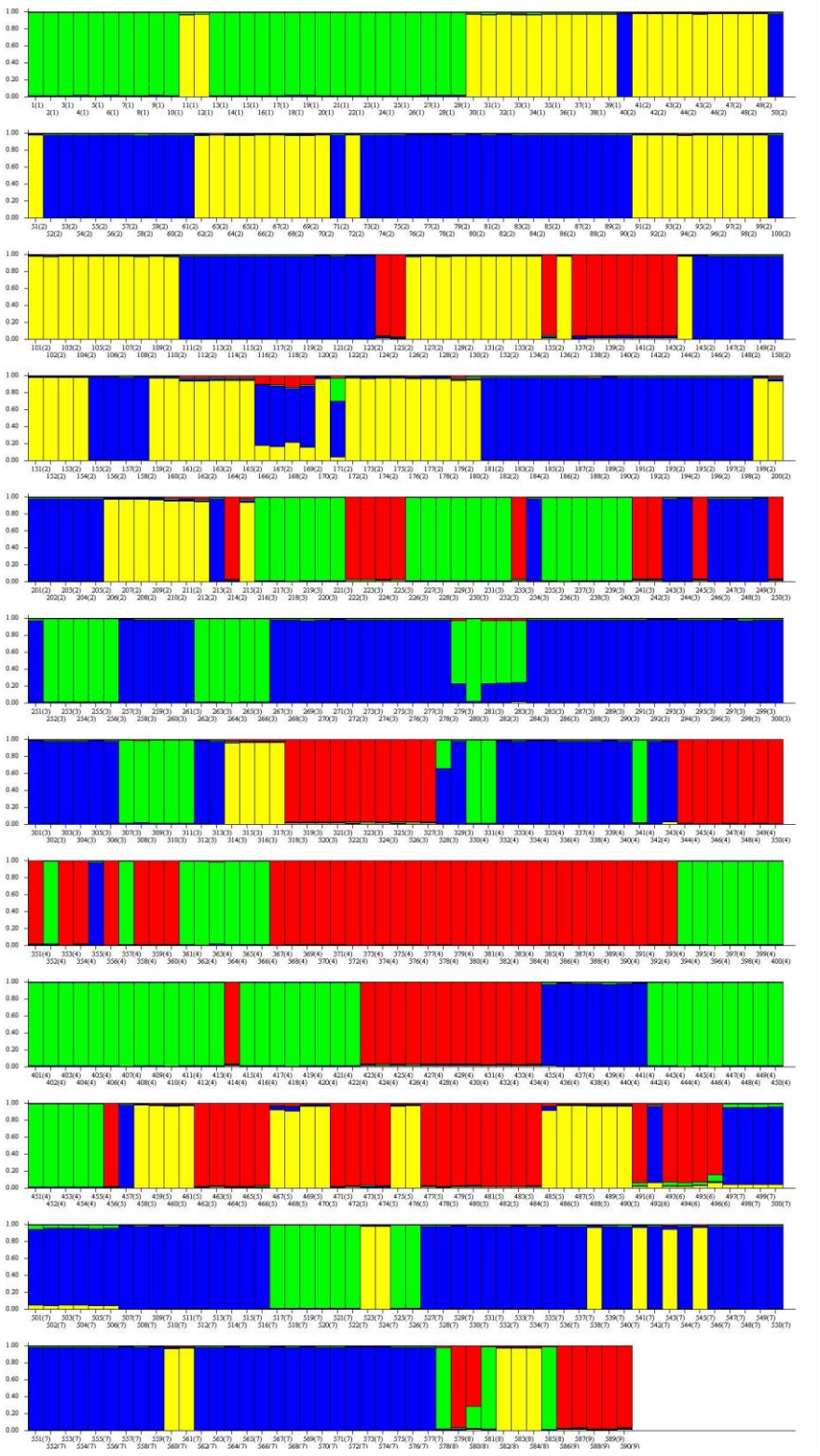


Figure 66. Barplot of Q assignments for each sample under K=4.

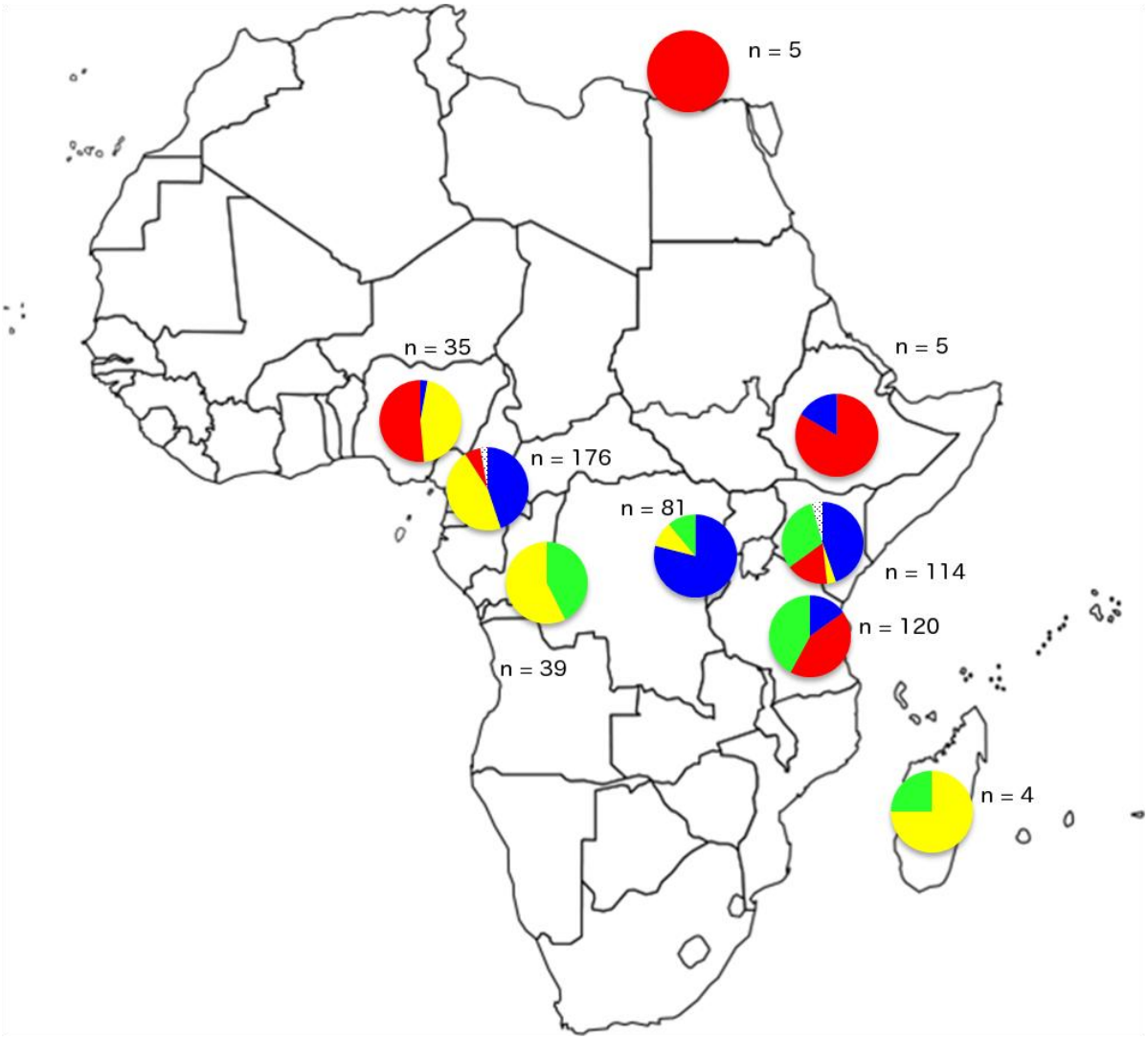


Figure 67. Map of the populations (K) identified by STRUCTURE (Pritchard et al., 2000). Each pie chart represents the distribution of samples (n = X) in each of the geographically predefined populations and the contribution of each of the four subclusters identified by STUCTURE.

ASSIGNMENT TEST AND DETECTION OF FIRST GENERATION MIGRANTS IN AFRICAN TARO

Gene flow between taro populations was tested with GENECLASS2 (Piry et al., 2004). This software uses three different methodologies to identify recent immigrants on the basis of their multilocus genotypes. Since populations were composed of a different number of individuals, frequency-based methods were not used in order to avoid bias in the mathematical modelling. Distance-based methods were also excluded because of the limited knowledge of the evolution model for the microsatellite loci investigated. In view of this, a Bayesian method was used (Rannala and Mountain, 1997) in which Monte-Carlo resampling was employed allowing for 10,000 simulated individuals. The results were plotted on a map (Figure 68), where arrows indicate movements of first generation migrants. Origin points only refer to the population source and cannot be taken as indicative of any specific location, and therefore should be considered to represent an area.

The results show several movements from the Pacific and Indo-Sri Lankan region to East Africa and Madagascar. Interestingly, the Mediterranean population represents the source population for some of the plants found in West Africa (Cameroon and Nigeria) as well as in East Africa (Kenya and Tanzania). However, due to the low number of samples present in the Mediterranean population this result has to be interpreted with caution. An internal equatorial exchange between the east and west of Africa is also

indicated by a double pointed arrow from the Nigerian and Cameroonian population to the central African population (Uganda, Burundi, east part of DRC), indicating a considerable movement of taro plants within Africa itself.

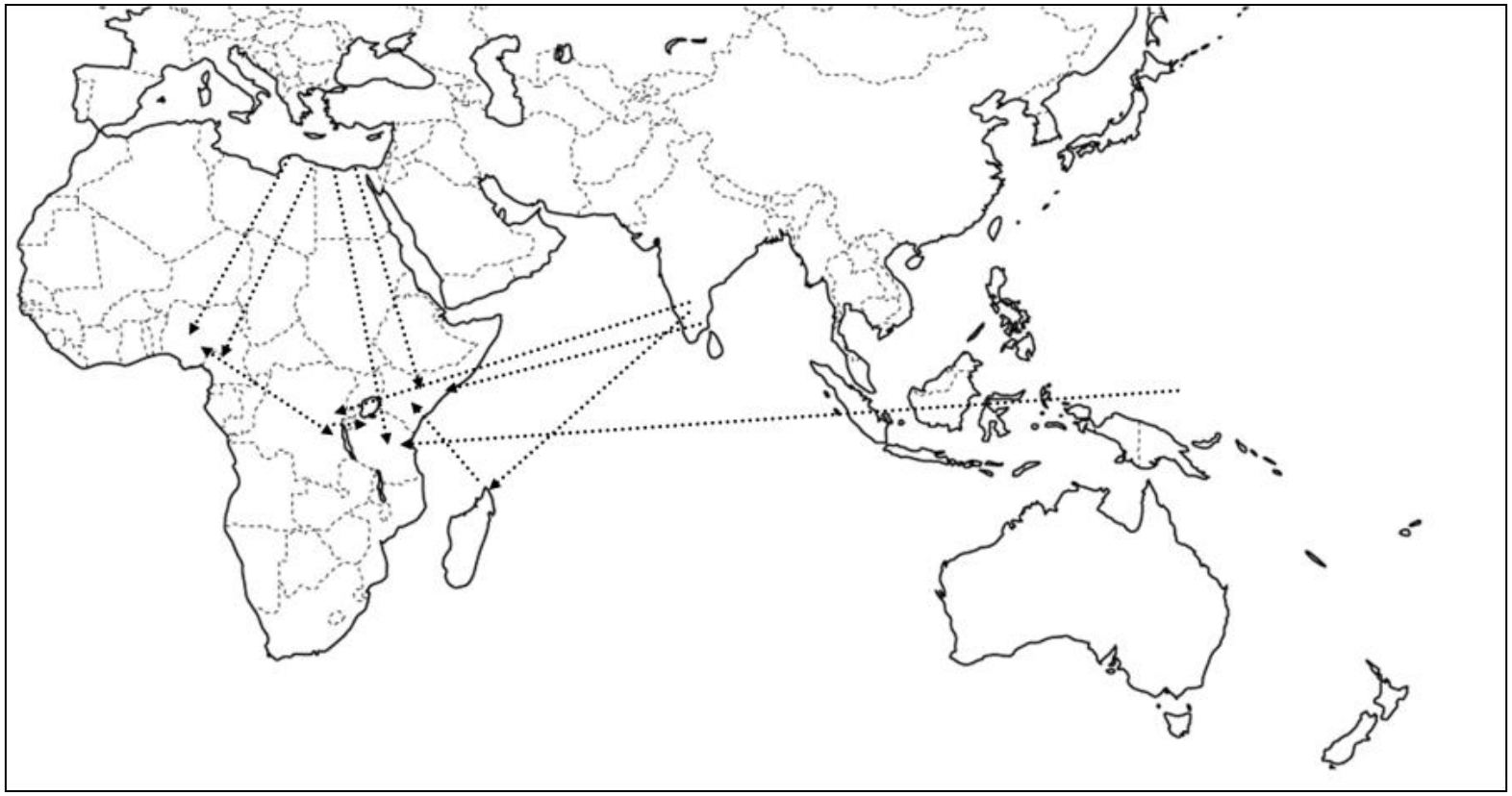


Figure 68. Map of first generation migrants in African taro based on results achieved with GENECLASS2 (Piry et al., 2004).

SUMMARY OF RESULTS

To analyse genetic variation in taro across Africa, and outside Africa, regions of the nuclear and chloroplast genomes were screened. Four chloroplast loci were investigated, and the *trnk* intron of the *matK* gene was eventually chosen for identification of the species, and to distinguish chloroplast lineages within taro. Sequences for 500 specimens were produced. In the 314 bp *trnK* segment there is a single nucleotide substitution G/A that divides taro into two groups. Full sequencing and characterization of the chloroplast genome by Ahmed et al. (2012; 2013) revealed the presence of three main chloroplast lineages in *Colocasia esculenta*, which are distinguished by mutations in the *matK* gene region, and at other loci. One lineage corresponds to a wildtype form of taro not seen or reported in Africa. The other two lineages, identified as the Indo-Pacific and Himalayan lineages include tropical and temperate-region cultivars of taro respectively. To relate the results of the outside survey with the present survey of African taro, a subset of identical DNA samples were analysed independently by both research teams (UK and NZ). In the African survey, 262 samples displayed a nucleotide substitution associated with the Indo-Pacific chloroplast lineage. This chloroplast genotype is labelled *mk1* in the present report. The remaining 238 plants displayed a nucleotide substitution associated with the Himalayan lineage, and is here labelled *mk2*. Since there was no prior reason to suspect such a division during

the initial African field survey and collection, the results suggests a similar abundance of both lineages in Africa. The plants collected in Africa display a range of traits in terms of leaf colour, mother corm morphology and side-shoot morphology. Leaf colour traits are not obviously related to chloroplast type, but corm and side-corm morphologies appear generally consistent with a division into temperate and tropical phenotypes (also known as eddoe and dasheen respectively).

To analyse the nuclear genome, 12 previously reported microsatellite loci were tested, and three were subsequently used for the wider survey of African samples (Xuqtem84, Xuqtem88b, and Xuqtem91). Genotyping of the microsatellite regions showed that two loci are highly polymorphic and very informative, namely Xuqtem84, which displays the repeat unit (CT)n, and Xuqtem88b, which displays the repeat unit (CAT)n. Sequencing of selected taro samples showed that Xuqtem88b contains another four repeat units that might provide additional length variation. This finding has to be taken into consideration when assuming a Stepwise Mutation Model for microsatellite evolution.

Locus Xuqtem91, which was previously reported to be a di-dinucleotide repeat unit, was also genotyped. The scoring of allelic profiles resulted in single bands 267-268 base pairs long, sufficiently similar to each other to indicate an "apparent" monomorphic state. When this locus was sequenced for the entire sample set, eight allelic forms were found. Seven alleles are of the same length,

but display between three and four nucleotide substitutions in and around the repeat unit region. This result highlights the need for care when using microsatellites, as poor understanding of variability in the repeat region could result in an incorrect interpretation of the results.

When the three loci were considered together, the taro samples from outside Africa (India/Sri Lanka, Japan and the Pacific region) displayed greater genetic diversity than the African sample set. When each locus is analysed at a population (or sample assemblage) level, greater diversity is found in the India/Sri Lanka population at locus Xuqtem84 and locus Xuqtem91. In contrast, locus Xuqtem88b indicates greater diversity in the Cameroon population.

The analysis of molecular variance was performed on twelve populations representing different geographical regions. In this study, it was not possible to collect the same number of samples in every country included. Small sample sets like those from the Mediterranean, Ethiopia and Madagascar were not grouped together as they represent very different geographical and historical regions. This study depended on original field collections (from the African mainland) and samples collected in an *ad hoc* manner by various collectors from across Asia and the Pacific.

The results for Africa show that differences within 'populations' account for most of the variance (71%), whereas differences between pairs of populations account for the remaining 29%. This result indicates considerable gene flow between populations, presumably in the form of cultivar transfers,

since cultivated taro is propagated vegetatively. The partitioning of variance thus indicates a large amount of plant movement between different geographical regions, which in turn must reflect both recent and historical trends in human interactions across the continent. Germplasm exchange was also noticed in the work carried out by van Rensburg et al. (2011). They compared taro plants collected in South Africa and Nigeria, and found that some plants collected from each country clustered closely to each other.

Multivariate analysis of the present data revealed an interesting substructure in African taros, when samples were classified according to source population and chloroplast type. Samples belonging to the same population did not all cluster together; rather, they are spread on the horizontal (first coordinate) and vertical (second coordinate) axes. In the second case, samples appear to cluster according to their chloroplast genotype, although some mixed samples occur in both groups. This result might reflect breeding and genetic mixing between plants associated with different chloroplast lineages. Such crossing could take place inside Africa, particularly in regions similar in climate to the tropical regions of Southeast Asia and the Pacific, where breeding by taro is common.

Cluster analysis also revealed two groups with a 100% bootstrap value; however, internal branches were poorly supported which may reflect a lack of differentiation within each group. Analysis of more loci is clearly needed to differentiate populations or clonal lineages among cultivated taros.

In order to further test for structure in African taro populations, a Bayesian approached was employed with the use of STRUCTURE (Pritchard et al. 2000). This software identified four (K) populations that tend to correlate with the two chloroplast genotypes, but not completely: (1) one group has a composition of 70% mk2 and 30% mk1; (2) a second group is 100% mk1; (3) a third group has a composition of 91% mk1 and 9% mk2; and (4) a fourth group is 100% mk2.

GENETIC ANALYSIS OF ARCHAEOLOGICAL TARO RETRIEVED AT QUSEIR AL-QADIM

RESULTS

Total genomic DNA was successfully extracted from a taro corm retrieved at Quseir al-Qadim, Egypt (Van der Veen and Morales, 2011). Designated primers were used to amplify the *trnk 3'* region within the *matk* gene. Amplification and sequencing were successfully completed. The chloroplast sequence retrieved confirmed that the corm is *Colocasia esculenta* (L.) Schott. In particular, the presence of a nucleotide substitution adenine A in the position 233 provides evidence that the sample investigated is likely to belong to the *C. esculenta* var. GP morphotype. In the 314 base pairs of the chloroplast region investigated, no other modification was present, which to a great extent reflects the relative conservation status of the chloroplast genome. The sequence retrieved is as follows:

>aTaro
CTTTACGGAAGAAGAAAAAGTGCTTTCTTTAATCTTACCAAGAATTTATTATCC
TTTACATAAGTTATATAGAGAACGCATTTGGTATTTGGATATTATTCGTATAAATGATTT
GGTGAACCATTTATGATTCATTAGTCATAAGACCATGTAAATGAAATCGAATAGAAAT
TCAAATTCTAAAGAGAGAAAAATGTCAGTCATTTTCATTCTGAAATGCCCATGCAGTA
AT**A**GTTGAATCAACTGAGTATTCAAGTTTCTTAGACTTTCTTTTCGGGATCTAAGTTTTA
GATGTATACATAGGGAAAGTCGTG

While the chloroplast region explored provided a reproducible sequence, sequencing of the nuclear microsatellites loci investigated did not produce readable and reliable sequences. Even though four loci were amplified

successfully, the sequencing of the nuclear microsatellites produced nucleotide sequences that cannot be fully assessed. Similarly, when fluorescent labels were added to the Forward primer, the fragmented nature of the taro corm was revealed in the genotyping analysis as shown in Table 19.

Table 20. Scoring of the alleles in the genotyped products.

Sample	FAM	PET Xuqtem110		FAM Xuqtem132		VIC Xuqtem228	
	Allele	Allele1	Allele2	Allele1	Allele2	Allele1	Allele2
aTaro	195.5	257.3		170.2		103.2	
aTaro	184	269.6		160		107.4	110
aTaro		259.4		155.3	169	87.4	
aTaro		266.2		147.6	170		
aTaro		269.8		174	176.8		
aTaro		296.6	300.2	157.4	169.5		
aTaro		253.6		147.5			
aTaro		245.7	263.6				

Table 19 shows that under the same conditions, the amplification of nuclear microsatellites produced segments of different lengths. This is also visible in the electropherograms reported below in Figure 69 for archaeological taro at locus Xuqtem228 and Figure 70 at locus Xuqtem110.

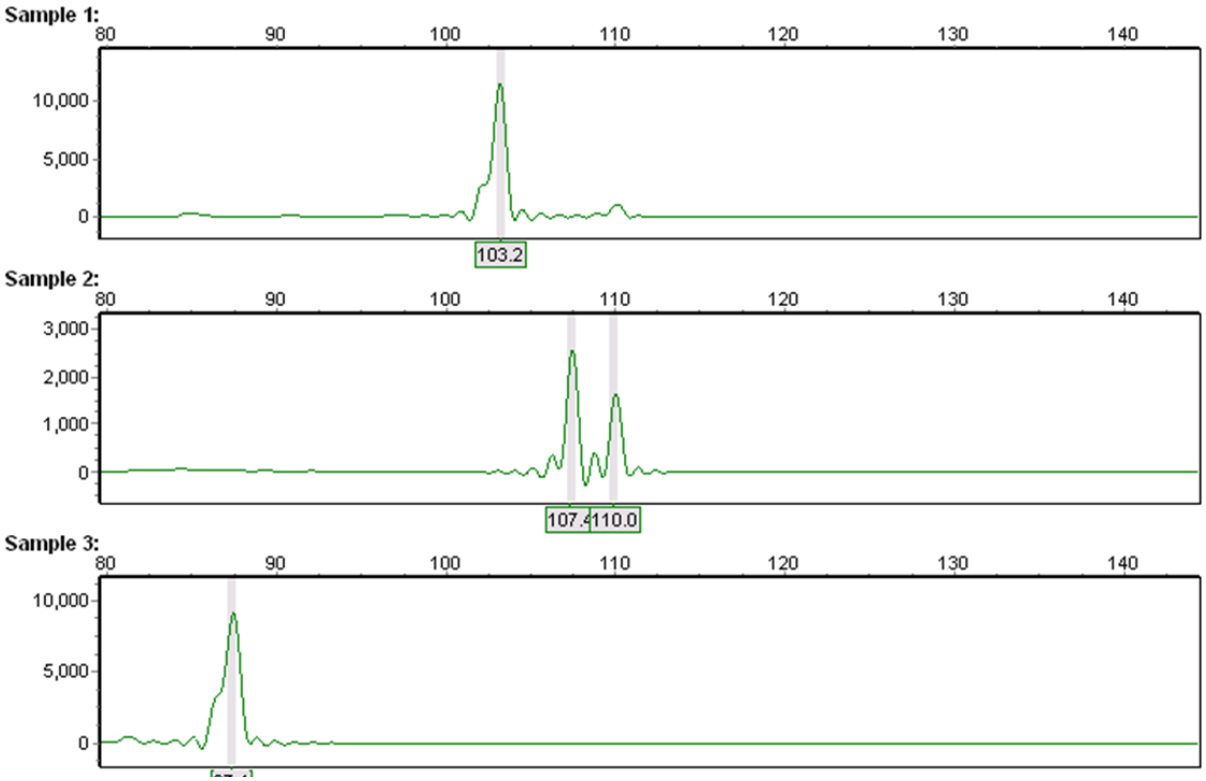


Figure 69. Electropherograms from an ABI310 Genetic Analyser showing alleles at locus Xuqtem228 for the archaeological taro.

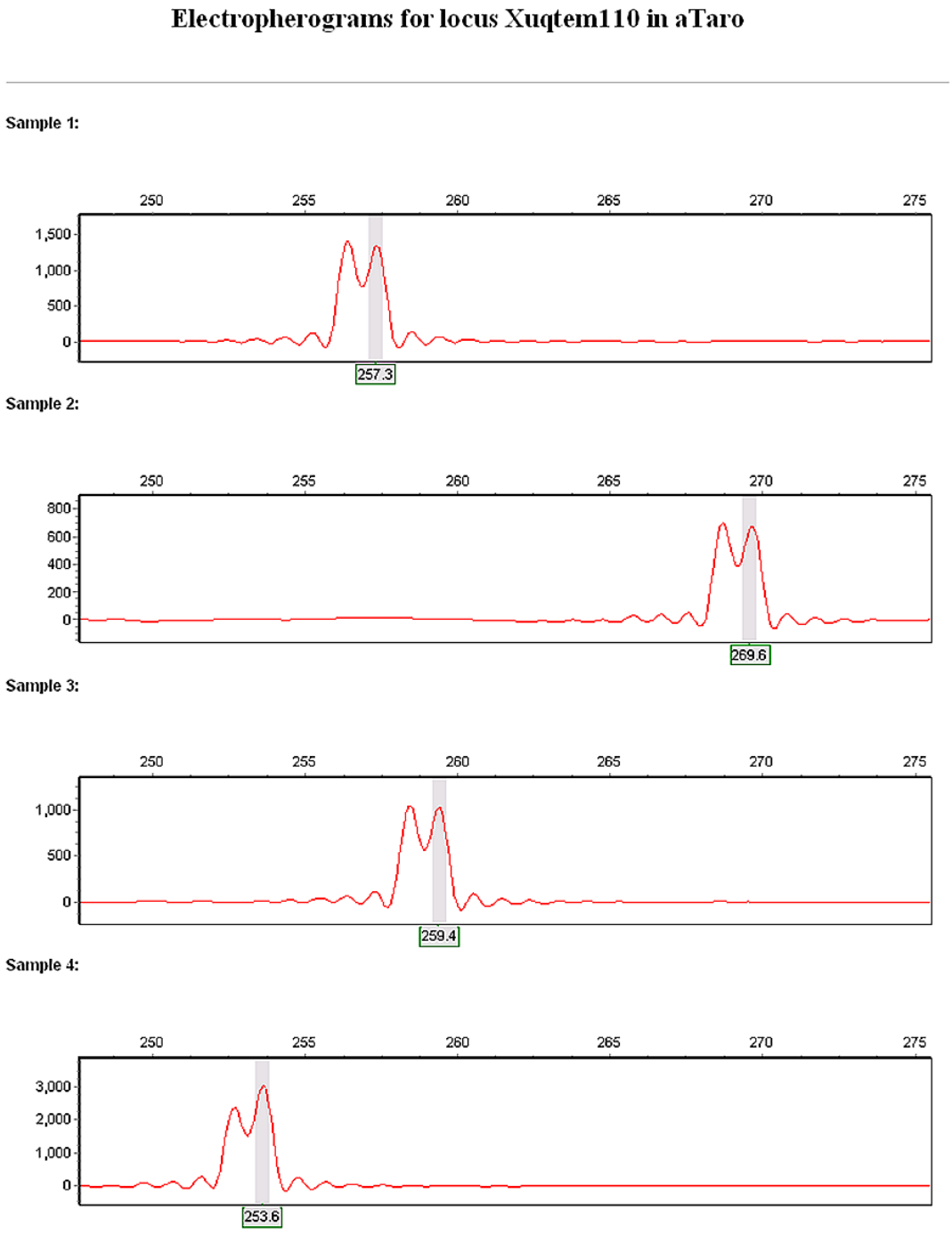


Figure 70. Electropherograms from an ABI310 Genetic Analyser showing alleles at locus Xuqtem110 for the archaeological taro.

In conclusion, the analysis of nuclear microsatellites has shown not to be appropriate for the investigation of the desiccated taro corm retrieved from

the archaeological site of Quseir al-Qadim, Egypt. The reasons for this result could be attributed not only to oxidative or hydrolytic reactions, which contribute to the shortening of ancient DNA fragments, but also to the impact of environmental factors on the preservation of the nuclear DNA, for example, high temperatures (Burger et al., 1999). As with the modern material, at the beginning of this study only a few chloroplast markers were available for screening of the nucleic composition of archaeological taro.

The work carried out by Ahmed et al. (2013) in the characterisation of suitable chloroplast loci provides a more in-depth investigation into the chloroplast molecule, meaning that future comparisons of the archaeological specimen found at Quseir with modern taro could give further clues as to its place of origin.

CHAPTER 6 TARO IN THE MEDITERRANEAN WORLD

INTRODUCTION

Historical and linguistic records of taro in the Mediterranean world have never been fully reviewed, yet there is no other region in or near Africa that has such a deep written history concerning taro. This written history is explored here as part of an attempt to understand both the entry of taro into the Mediterranean, and the possible routes of dispersal of taro from the Mediterranean into Africa, and/or vice versa.

Two different types of sources have been used here. The first is a search engine tool based on the *Thesaurus Linguae Graecae* (*TLG*) and *Thesaurus Linguae Latinae* (*TLL*) which are both available online. The *TLG* and *TLL* are digital collections of all surviving texts written in Greek (*TLG*) and Latin (*TLL*) during antiquity (to the fall of Constantinople in 1453 AD for Greek, to the 7th century for Latin). They were created by the University of California, Irvine, and the Bavarian Academy of Sciences and Humanities, Munich, respectively. These tools allow systematic research to be conducted on any term. More specifically, the Greek word *colocasia* – κολοκάσιον (plur. κολοκάσια) and its Latin form *colocāsium*, *-ī* n. or *colocāsia*, *-ae f.* –, the Greek name *Egyptian bean* – κύαμος Αἰγύπτιος and its Latinized version *cyamos Aegyptius*, the Greek term *ouingon* – οὔϊγγον, οὔϊπον, οὔϊτον (the spelling varies), and its Latin form

oetum, *-ī* n. –, and the Greek name *aron* – ἄρον, and its Latin form *aros*, *-ī* f. and *arum*, *-ī* n. – were fully investigated in the texts where these terms are included. A comprehensive philological discussion of names associated with taro is not attempted.

The second type of source is Late Medieval to recent historical literature, most often the works of herbalists and botanists. Authors and works of particular importance are Matteo Silvatico (*Opus Pandectorum*, 1317), Gaspard Bauhin (*Pinax theatri botanici*, 1623), Pietro Matthioli (*Commentarii*, 1565) and Carolus Linnaeus (*Species Plantarum*, 1753). These authors summarised European knowledge of plants at different times over a period of approximately 400 years. Further commentaries published in the 18th and 19th centuries were also consulted.

Taking into account the classical nature of the original texts, selected passages have been translated into English where necessary. However, when the original language was thought to be critical for the interpretation of the text, it has been reported in full.

The reader should bear in mind that before the official naming of the botanical species by Linnaeus in 1753, names and descriptions of plants used in the literature cannot necessarily be associated with modern scientifically recognised plants, unless clear representations were given. Therefore, in order to avoid confusion, I will only use the word taro when the interpretation of the above mentioned Greek and Latin terms are thought to

refer to *Colocasia esculenta* (L.) Schott, as studied in this research. In all other instances, an interpretation of the Greek and Latin terms has been given based on references found in the literature.

In this Chapter, a map of taro in the Mediterranean area will first be presented. The map was compiled according to records of taro present in the botanical literature, floristic archives, and in ethnographic and agriculture reports. Appendix 1 at the end of this document reports these sources. Since distribution maps can suggest historical patterns of dispersal, the map was constructed to visualise the distribution of taro in the Mediterranean area and assess the possibility that this area represented a route of introduction of taro into Africa.

This chapter subsequently assesses the presence of the word *colocasia* in Greek and Latin texts. This will be followed by a section on the term *ouingon* and finally a review on the presence of the term *aron* in the Greek and Latin literature. Because the latter is found extensively in the classical literature, only key texts have been chosen. The order in which the records have been presented is as much as possible chronological, though in some instances, temporal jumps have been necessary to link commonalities and patterns in the dataset.

Table 20 lists early authors, their works and abbreviations used in this text. The known or approximate date of each work is also indicated.

Table 21. List of authors, texts and abbreviations mentioned in this chapter.

AUTHOR	DATE	TEXT
Herodotus (Hdt.)	5th century BC	*Histories* (*Historiae*)
Corpus Hippocraticum (CH)	5th-4th century BC	*On Ulcers* (*De Ulceribus =Ulc.*); On Diseases (*De Morbis = Morb.*)
Aristotle (Arist.)	4th century BC	*Inquiries on Animals* (*Historia Animalium = NA*)
Theophrastus (Theophr.)	4th-3rd century BC	*Enquiry into Plants* (*Historia Plantarum = HP*)
Nicander of Colophon (Nic.)	2nd century BC	*Georgics* (*Georgica*)
Virgil (Verg.)	1st century BC	*Eclogues* (*Eclogae = Ecl.*)
Columella (Col.)	1st century AD	*On Agriculture* (*De Re Rustica*)
Pliny the Elder (Plin.)	1st century AD	*The Natural History* (*Naturalis Historia = NH*)
Dioscorides Pedanius (Dioscor.)	1st century AD	*Medical Materials* (*Materia Medica = MM*)
Martial (Mart.)	1st-2nd century AD	*Epigrams* (*Epigrammata*)
Galen of Pergamon (Gal.)	2nd century AD	*On the Properties of Foodstuffs* (*De AlimentorumFacultatibus= Al. Fac.*)
Athenaeus of Naucratis (Ath.)	2nd- 3rd century AD	*The Banquet of the Learned* (*Deipnosophistae*)
Apicius (Apic.)	2nd- 4rd century AD	*On the Subject of Cooking* (*De Re Coquinaria*)
Oribasius (Orib.)	4th-5th century AD	*Medical Collections* (*Collectiones medicae*)
Palladius (Pall.)	4th century AD	*Agricolture* (*Opus Agriculturae = Op. Agr.*)
Hesychius of Alexandria (Hsch.)	5th century AD	*Lexicon* (*Lexicon*)
Paul of Aegina	7th century AD	*Medical Compendium* (*De Re Medica*)
Isidore of Seville	7th century AD	*Etymologies* (*Etymologiae* or *Origines = Orig.*)
Mesue the Elder	8th-9th century AD	*Liber de Simplicibus*
Isaac Israeli	9th-10th century AD	*Diaetae Particulares*
Avicenna (Ibn Sīnā)	10th-11th century AD	*The Canon of Medicine*
Matteo Silvatico	1317	*Opus Pandectarum Medicinae or Pandectae Medicinae*
Serapion the Younger	12th century AD	*The Book of Simple Medicaments* (*Liber aggregatus in medicinis simplicibus*)
Nicolò Roccabonella	1445-48	*Liber de Simplicibus*
Luigi Anguillara	1561	*Semplici dell'eccellente*
Pietro Andrea Matthioli	1565	*Commentarii*
Carolus Clusius	1576	*Rariorum aliquot stirpium per Hispanias observatarum historia*
Andrea Cesalpino	1583	*On Plants* (*De Plantis*)
Prospero Alpini	1592	*De Plantis Aegypti liber; De Plantis Exoticis*
Francesco Fantasti	1714	*Fiore della Colocassia*
Carl Linnaeus	1753	*Species Plantarum*
Alphonse De Candolle	1883	*L'origine des plantes cultivées*
Romualdo Pirotta	1908	*Annali di botanica*
Liddell–Scott–Jones	1843- 1996	*A Greek–English Lexicon*
Beeks, R; van Beek, L	2010	*Etymological Dictionary of Greek*

PRESENCE OF TARO IN THE MEDITERRENAEAN

Historical botanical records show that taro was widely distributed in the Mediterranean in the past (Figure 71). It is today commonly cultivated in Egypt, where it is known by the Arabic name الـ قـ لـ قاس (qolqas), and also in Cyprus, where it is known as kolokasi (Matthews, 2006). It is still present in Turkey, Greece, and Lebanon, where it is used in local cuisine as a traditional food. The plant is still present in the wettest part of Libya, specifically in Wadi Darnah, the only permanent river in Libya, which is located near the ancient Greek city of Cyrene (near modern Shahhat), a historical commercial hub during Greek and Roman times. In an Arabic manuscript dated to the 13th-14th century AD found in the Library of Alger, taro was included on a list of medicinal plants (Meyer, 1881: 1). In this manuscript, taro is known as *Louf*, *Siaoun* and *Kolkace*, or commonly *Colocasie* or *Colocasse* (ibid. pag. 45-49). In addition to these names, Quézel et al. (1962) reported that in Algeria the names *Ker*, *Kour* and *Kolhas* were used. In this country, Battandier and Trabut, (1885) and Mayer (1957) recorded it growing in the area of Cape Rosa. Täckholm and Drar (1941: 367) reported taro to be growing also in Morocco, although absence from modern flora could indicate that the plant has now disappeared in this region. It is also present in Italy where it is still known as *Aro d'Egitto* or *Ara d'Egitto* (*Arum of Egypt*), and *Trombe del Paradiso* (*Heaven's Trumpets*), a name which derives from an old medieval term *pamphina paradisi*

(Cesalpino, 1583) used in the past for this plant. In particular, the plant is naturalised in Sardinia, Sicily and Calabria, which are the most southern Italian regions. Interestingly, taro was recorded in the early 20th century by the Sicilian vernacular name *Curcuraci* (Cavara, 1905: 139), which is similar to the terms *kour* and *kúrkum* recorded for taro in 20th century Algeria (Quézel et al., 1962) and Yemen (Schweinfurth, 1912).

In Sardinia, taro is also known as *Elephant ears*, but botanists generally refer to it by the old scientific name *Colocasia antiquorum* (author's field notes). The plant has also been recorded in Albania, the Balkans, and the Canary Islands, and it is still present in the Balearic Islands, Portugal, and Spain. In Spain, Clusius (1576) noted the names *inhame*, *alcoleaz* and *Manta de nuestra señora*, (cfr. Matthews, 2006 Manto dela Madonna) for taro. In the region of Seville, taro is becoming an invasive plant (García-de-Lomas et al., 2012).

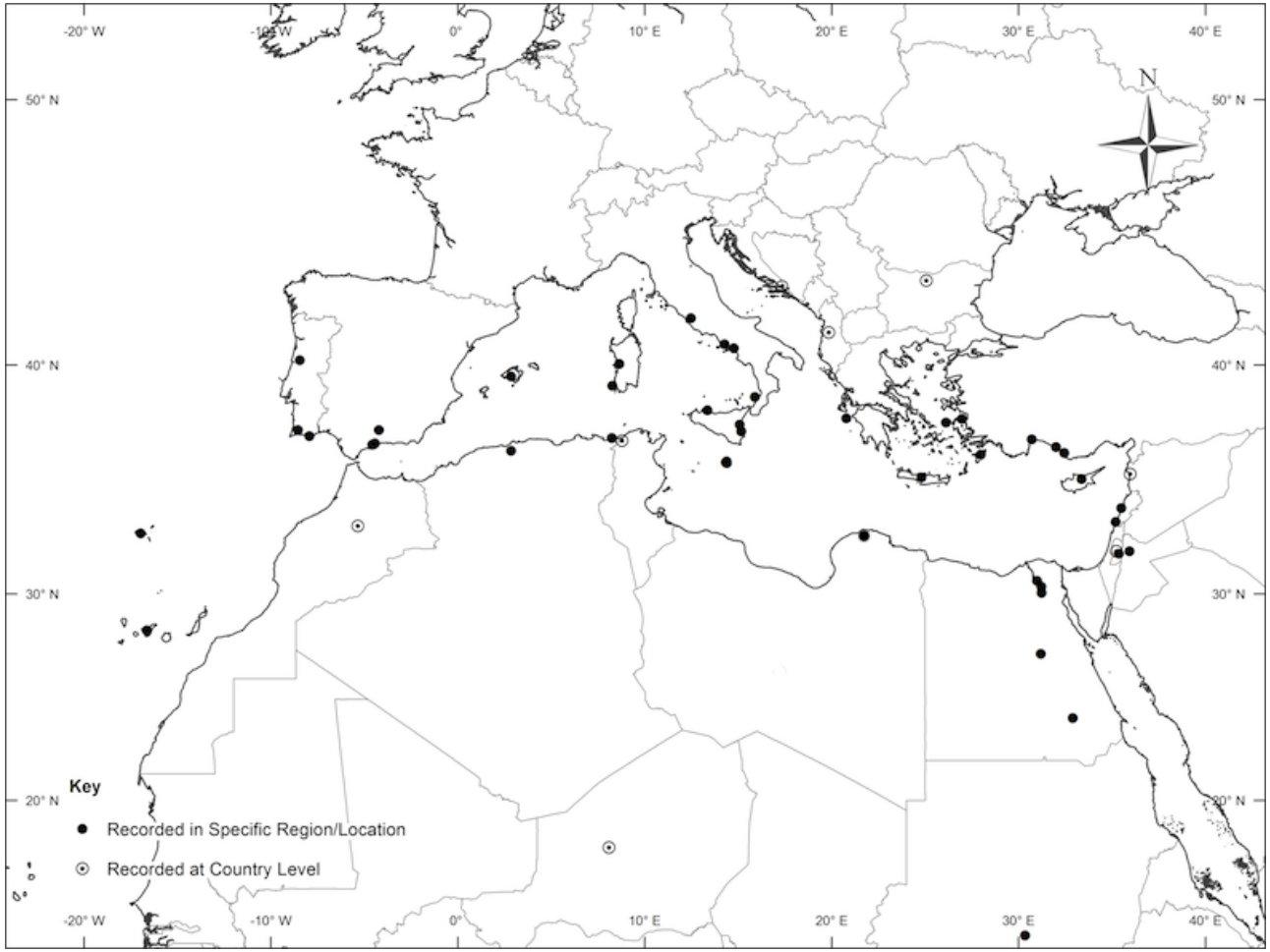


Figure 71. Map of the distribution of taro in the Mediterranean region, based on sources reported in the Appendix 5 at the end of this chapter.

THE TERM *COLOCASIA*

The scientific (Latin) name for taro, *Colocasia esculenta* (L.) Schott, originates in the Mediterranean area. The species name *esculenta* is a Latin term meaning 'edible', and the name *Colocasia* is a Latin vernacular name for taro that obviously derived from the Greek term κολοκάσια (*kolokasia*). The origin of the Greek name has been debated for a considerable time (Candolle, 1883; Thiselton-Dyer, 1918; Portères, 1960; Watson, 1983). Exactly how this name was first used in antiquity is a matter of continued uncertainty.

The following authors all refer to *colocasia*: Nicander (2nd century BC), Virgil (1st century BC), Dioscorides (1st century AD), Pliny the Elder (1st century AD), Columella (1st century AD), Martial (1st century AD), Galen (1st-2nd century AD), Athenaeus (late 2nd-3rd century AD), and Palladius (4th -5th century AD). Generally the term was used to refer to a plant that was known to be growing in Egypt and that was also cultivated in Italy. The name is also found in the Apicius collection of recipes (4th- 5th century AD) (Vehling, 1977). However, descriptions associated with the name suggest that the plant referred to was a kind of water lily recognised by scholars as the sacred Indian lotus, *Nelumbo nucifera* Gaertn. (Figure 72; see Woenig, 1897; Burkill, 1938; Täckholm and Drar, 1941). The term κολοκάσια and its cognates in Latin and Arabic are widely used to refer to taro in the Eastern Mediterranean today. In the past, the name may have had a less specific connotation, and

could have been used for more than one plant with an edible underground storage organ.

Figure 72. Indian Lotus plant (*Nelumbo nucifera* Gaertn.) Seed pod and edible beans are visible. Photo by P.J. Matthews (South Korea, August, 2013).

The term *colocasia* appears to have been used for the first time by Nicander of Colophon (2nd century BC) and Diphilus of Siphnos (3rd-2nd century BC) in a passage reported by Athenaeus of Naucratis (2nd century AD) in *The Banquet of the Learned* (*Deipnosophistae*) (Thiselton-Dyer, 1918; Matthews, 2006). *The Banquet of the Learned* is a collection of 15 books written in the form of dialogues amongst the notorious participants of banquets held at the house of Laurentius, a noble Roman. Almost all of the original work has survived to the present day, although the first two books and other sections that follow are found in the form of epitomes (Yonge, 1854). The first part of book III is also an epitome and refers to the *kiboria* (κιβώριον n., pl. κιβώρια), a name

used to describe the seed-vessel of the lotus plant (Ath. 3,72a-b). According to Athenaeus, when discussing the *Egyptian bean*, Nicander refers to a tuber that the Alexandrians call *kolokasion* (Ath. 3,72b). In the following, parts written in standard font represent the voice of Athenaeus writing, while those written in italics represent the voice of Nicander:

> "Lotus pod (κιβώρια). Nicander in his *Georgics*:
>
> «*Sow the Egyptian variety of bean, so that in summer*
> *you can produce garlands with its flowers, and when the pods full of ripe fruit have fallen,*
> *put them into the hands of young men*
> (72b) *who are dining and have long been desiring them.*
> *As for the roots, I boil them and serve them at banquets*». (Fr. 81)

Nicander uses the term "roots" for what the Alexandrians call κολοκάσιον. As he himself says:

> *Having stripped the κολοκάσιον from the bean and cutting it up*. (Fr. 82)
> (Nic. *apud* Ath. 3,72a-b = frr. 81-82 Schneider) (Translation from Sharples, 1995)

Athenaeus continues to report Theophrastus's description of the Egyptian bean as a "reed-like" type of aquatic plant that grows in marshes and swamps, with large leaves, a big pink flower, and hard tubers that are eaten roasted, boiled or raw (Ath. 3,72b-72d). Athenaeus asserts that also Diphilus of Siphnos refers to κολοκάσιον as the root of the *Egyptian bean*. He describes the food as tasty and nutritious, though hard to digest, and the beans as a laxative or a cause of flatulence (Ath. 3,72d-73a).

By the 5th century BC, Herodotus (2,92,4), in a section on plants growing in the Nile, described plants known as *lotos* (λωτός), one having a pink flower and a structure similar to a wasps' nest containing seeds that were eaten both fresh and dried (Lloyd and Fraschetti, 1989). This description endures over time and in the *Materia Medica* of Dioscorides (*MM* 2,128), as well as in the *Naturalis Historia* of Pliny (*NH* 21,87) the word *colocasia* appears as a term used for the roots of the *Egyptian bean*:

> The Egyptian bean (which some call *pontica)* grows abundantly in Egypt, Asia and Cilicia, and is found in marshy places. It has a leaf as great as a hat, a stalk the height of a foot, about the thickness of a finger. The flower is a rose colour, twice as big as the flower of a poppy. Having done blooming it bears pods similar to little bags, in each of which is a little bean (standing out above the covering) similar to a little bladder. It is called *ciborium* or *cibotium* (as we should say *loculamentum*) because the setting of the bean is made when it is put in moist land and so left in the water. The root is thicker than that of the reed and lies underneath. This is used either boiled or raw and is called *collocasia*. The bean itself is also eaten green, but when dry it grows black and is bigger than the Greek one, astringent, and good for the stomach. As a result the meal that is made from them, sprinkled on instead of polenta, is good for dysentery and the abdominal cavity, and it is given as a porridge. The husks work better boiled in *mulsum* [honey, water and wine] and three cupfuls of it given to drink. The green in the middle of them is bitter to taste, and good for earache, pounded into small pieces, boiled with *rosaceum* and dropped in the ears. (Dioscor. *MM* 2,128; translation by Osbaldeston and Wood, 2000)

Desiccated seeds of *Nelumbo nucifera* were retrieved at Berenike, Egypt and were dated to the 1st- 2ndcentury AD (Cappers, 2006), confirming that the plant must have been known in Egypt in the Classical period.

Athenaeus, in the chapter on *kiboria*, refers to a shrine in Sicyon (Greece) that was dedicated to *Athena Kolokasia.* This is the only known reference to the existence of this shrine; no archaeological remains of the shrine appear to have been discovered.

The epithet *kolokasion* has been found on a marble plaque dedicated to a Jewish man dated to the 4th century AD, possibly from Palestine, whose nickname was κολοκάσιον. The name was interpreted by Schwartz (1989) as a reference to a plant, and to identify the plant he referred to the edible root of the *Egyptian bean* mentioned by Athenaeus. There is nothing in the plaque itself to support any particular interpretation of the meaning of the name. Schwartz has no new evidence, but the existence of the name at this time and place is significant. Peter Matthews also noted that in Cyprus the name *kolokasi* (possibly spelled *colocasi*) was adopted as a formal surname by some families when the British administration forced islanders to use the surname, first name system. He also notes that the name had been given to an ancestor because of his greedy appreciation of taro served at a wedding banquet (Peter J. Matthews's pers. comm.).

Athena Kolokasia is sometimes translated as 'Athena of the edible tubers', and referring to κολοκάσια in respect of *Nelumbo nucifera* and to *Colocasia esculenta*, Salvagno (2001) highlights the possibility that *kolokasion* could have been a general term for tubers, testifying to an early presence of taro in this region. The use of generic terms for different things, especially in

regard to plants, is common in folk taxonomies. For example, in modern Greek the word μολόχα ("molocha"), meaning mallow, originally indicated plants in the family Malvaceae, but is also used by people as generic terms for certain ornamental garden plants such as petunia, peony or geranium, which actually do not have anything in common with the mallow (Alkiviadis Ginalis, University of Oxford, pers. comm.). At present, in Africa, most names applied to corms of taro (*Colocasia esculenta*) in the field are also applied to yautia (*Xanthosoma saggittifolium* (L.) Schott). The leaves and corms of these plants are similar in appearance, have similar uses, and are produced using similar agronomic practices (see Chapter 4 Ethnobotanical observations of taro in Africa).

Contrary to Portères's conclusion (1960) that the term *colocasia* was not present before the 1st century AD, this term appears in the *Eclogues* of Virgil (*Ecl*.4, 20). The *Eclogues* are a collection of ten pastoral poems that Virgil wrote between 42 and 39 BC; *Eclogues* IV has been considered the most enigmatic because the central figure is a mysterious child who will lead to a golden age, a theme often interpreted as a pagan prophecy of the coming of Christ (Arnold, 1994):

> *At tibi prima, puer, nullo munuscula cultu*
> *errantis hederas passim cum baccare tellus*
> *mixtaque ridenti colocasia fundet acantho.*
> (Verg. *Ecl*. 4,18-20)

"But newborn boy, for you, these presents shall pour forth,
Cyclamen first, with ivy spread all over earth,
then colocasia mixed with acanthus smiling."
(Translation from Krisak, 2010).

For Virgil, *colocasia* is a gift given by nature to the unknown child, and while scholars usually identify Virgil's *colocasia* as *Nelumbo nucifera* (Conington, 1884; Clausen and Marón, 1994; Volk, 2008), for Martyn (1749), an accomplished botanist, this was clearly a reference to the taro that was growing in Italy at the time Virgil wrote his poem. Fée (1822a,b) expanded on this interpretation, although with some reservation. He was on the one hand inclined to think that Virgil was making use of an analogy to the lotus plant, likened to a beautiful flower that the Earth produced to show its joy for the mysterious newborn child. However, he noted that the original text contained words that did not suggest such great splendour, but instead talked about first (*prima*), small presents (*munuscula*), the merit of which was to have been produced without culture (*nullo culto*). It is the choice of words in Virgil that persuaded Fée to lean more towards the interpretation of *colocasia* as taro.

From what we know of the plant, it would seem that Virgil's *colocasia* does not refer to the roots as indicated in Nicander and Diphilus, but becomes the name for flowers or a whole plant.

Following Virgil's work, in the 1st century AD the word *colocasia* appears in several texts. In *On Agriculture* (*De Re Rustica*) Columella referred

to *colocasia* to indicate plants used only to decorate the middle part of ponds "together with other green stuff which generally grows in the water and provides shade for the haunts of the waterfowl" (Forster and Heffner, 1968). There is still a practice, especially in Italy, of planting taro on raised areas in the middle of ponds, often with lotus plants in the surrounding water (author's personal observation). Unfortunately, the brief and undescriptive passage of Columella does not allow a full interpretation of the plant. However, the reference to the presence of 'other green plants' growing in ponds may indicate that *colocasia* was itself appreciated as a green plant (as taro is today), rather than as a flowering plant.

Martial, who is the most irreverent Roman author, also mentions *colocasia*, and in the *Epigrams* describes the plant as having a slender stalk (8,33,13), and as a vegetable with strong threads and stubborn fibres (13,57):

Colocasia

Niliacum ridebis holus lanasque sequaces,
inproba cum morsu fila manuque trahes.
(Mart. 13,57)

"**Colocasia**
You will laugh at the vegetable from the Nile and its clinging fibres,
when you pull at its naughty threads with mouth and fingers."
(Translation by the author).

While Ker (1920) translated *colocasia* in this passage as the *Egyptian bean* (i.e. lotus, *Nelumbo nucifera*), Shackleton (1993) identifies it as taro, while

noting that there is some confusion with *Nelumbo nucifera*. Unlike those of taro, which once cooked are soft (Pieroni et al., 2007; Matthews's pers. comm.; author's observation), the rhizomes of Southeast Asian lotus are stringy (Li et al., 2010; Liu et al., 2012), which may suggest that the passage refers to the latter plant.

For Pliny the Elder (*NH* 21,87), *colocasia* was 'most noble' (*nobilissima*). Drawing from Theophrastus' and Dioscorides' descriptions, in a section on Egyptian plants, he describes *colocasia* as a plant also known as *cyamon* (from the Greek κύαμος = bean), that has a beautiful thyrse that stands out of its big leaves, which resemble those of the *personata*:

> *In Aegypto nobilissima est colocasia, quam cyamon aliqui vocant. Hanc e Nilo metunt, caule, cum coctus est, araneoso in mandendo, thyrso autem, qui inter folia emicat, spectabili, foliis latissimis, etiam si arboreis conparentur, ad similitudinem eorum, quae personata in nostris amnibus vocamus, adeoque Nili sui dotibus gaudent, ut inplexis colocasiae foliis in variam speciem vasorum potare gratissimum habeant. Seritur iam haec in Italia*. (Plin. *NH* 21,87)

> In Egypt the most famous plant of this kind is the colocasia, called by some cyamos; they gather it out of the Nile. The stalk of the stem when boiled and chewed breaks up into spidery threads, but the stem itself is handsome, jutting out from leaves which, even when compared with those of trees, are very broad, similar to the leaves called personata which are found in Italian rivers. So much do the people of the Nile appreciate the bounty of their river that they plait colocasia leaves into vessels of various shapes, which they consider make attractive goblets. The colocasia is now grown in Italy. (Translation by Jones, 1969)

This is probably one of the most important and yet unclear passages in which the term *colocasia* is found. Grandsagne (1832) who translated and

commented on the *Natural History* of Pliny, regarded taro as to the c*olocasia* mentioned by Virgil, Palladius, Athenaeus, Martial and as the *Cyrenaic aron* of Galen, a subject that will be discussed later in this chapter. Jacques André, a brilliant French scholar who has dedicated his life to the study of ancient texts, believes that only the last sentence referred to taro (1956, 1981, 1985, 2010). Lechi (1984) is of the same opinion, recognising in the first part of the description the Egyptian bean, and subsequently taro. However, it is also possible that the name *colocasia* was already a common term for both the lotus plant and taro. In this regard, Pliny gives us a hint when he compares the leaves of *colocasia* to the ones of the *personata*, a plant that is generally believed to be *Arctium lappa* L. (Lechi, 1984), the heart-shape leaves of which are more similar to those of taro than to the lotus plant.

In *On the Properties of Foodstuffs* Galen referred to κολοκάσια and κιβώρια (the lotus pod) only as plants that can be eaten in case of famine, and that can be stored in vinegar. "It is clear", continues Galen, "that as well as giving little nutriment to the body, these are all unwholesome except, as I said, the spiny plants that have just emerged from the ground" (39,623; translated by Powell, 2003).

In the 4th century AD, Palladius wrote *Agriculture* (*Opus Agriculturae*), in which he mentioned c*olocasia* twice, the first time (*Op. Agr.*3,24,14) as a plant from which bulbs are set in the month of February:

> *Affiant umidum locum, pinguem, maxime inriguum. Circa fontes laetantur et riuos nec de soli qualitate curant, si perpetuo foueantur umore. Frondere prope semper possunt, si tamquam citreta tegumentis defendantur a frigore.* (Pall. *Op. Agr.* 3,24,14)
>
> It likes a moist rich situation well watered. It grows luxuriant round fountains and rivers, and does not care about the quality of the soil if it is cherished by perpetual moisture. It may be kept almost always in a flourishing condition if it is defended from the cold. (Translation by Owen, 1807)

The second time *colocasia* is only listed in a section on plants to be planted in gardens in March (*Op. Agr.*4,9,5). André has always accepted that this *colocasia* is taro (1956, 1981, 1985, 2010). The planting conditions described by Palladius fit perfectly with taro, which is always grown in soil to which water is added, or next to water, in contrast to lotus, which grows in water (P.J. Matthews pers. comm.).

Finally, the use of *Colocasia* is recorded in the classic Roman food recipes book *On the Subject of Cooking* (*De Re Coquinaria*). Despite the author being referred to as Apicius, it seems it is more likely to be a collection of several people's contributions written between the 2nd and 5th century AD (Vehling, 1977). Vehling (1977) believes that in the manuscript, the word *colocasia* is found under several forms such as *coladium*, *coledium*, *coloesium* and *colesium*, but that they are all misspellings of the same word *colocasia*. The book describes how the corms of *colocasia* are used as a vegetable to bulk out meat or fowl dishes, suggesting it was not a major element in the diet of ordinary Romans. For Gentilini (2004) and Vehling (1977) this is taro, and the

recipes used can be easily applied to taro.

Readers may wish to consider the recipes that include *colocasia* in *De Re Coquinaria*, as translated by Vehling (1977). Although inconsistent, Vehling's translation is reported as he presented it. His use of the modern term 'dasheen' rather than *colocasia* has also been left as shown in the translation. Square brackets indicate notes made by Vehling. Text in bold has been highlighted by the present author.

(74) *Aliter cucurbitas iure* ***colocesiorum*** (Barley Pumpkin like dasheen)

Boil the pumpkin in water like **colocasia**; grind pepper, cumin and rue, add vinegar and measure out the broth in a saucepan. The pumpkin pieces [nicely cut] water pressed put [are arranged] in a saucepan with the broth and are finished on the fire while the juice is being tied with a little roux. Before serving sprinkle with pepper.

(172) *Tisana sive cremore* (Barley broth, pap, porridge, gruel)

Crush barley, soaked the day before, well washed, place on the fire to be cooked [in a double boiler] when hot add enough oil, a bunch of dill, dry onion, satury and **colocasium** to be cooked together because for the better juice, add green coriander and a little salt; bring it to a boiling point. When done take out the bunch [of dill] and transfer the barley into another kettle to avoid sticking to the bottom and burning, make it liquid [by addition of water], both, milk, strain into a pot, covering the tops of the **colocasia**. Next crush pepper, lovage, a little dry flea-bane, cumin and sylphium stir it well and add vinegar reduced must and broth; put it back into the pot, the remaining **colocasia** finish on a gentle fire. (Recipe repeated in n. 200 *Alicam vel succum tisanae sic facies* Barley broth)

(216) *Aliter gruem vel anatem assam* (Roast crane or duck)

Pour over [the roast bird] this gravy: crush pepper, lovage, origany with broth, honey, a little vinegar and oil; boil it well, thicken with roux [strain] in this sauce place small pieces of parboiled pumpkin or **colocasium** so that they are finished in the sauce; also cook with it chicken feet and giblets [all of which] serve in a chafing dish, sprinkle with fine pepper and serve.

(244) *Pullum elixum cum colocasiis elixis* (Chicken and dasheen)

The above sauce is also used for this dish. Stuff the chicken with [peeled] **dasheens** and [stoned] green olives, though not too much so that the dressing may have room for expansion, to prevent bursting while the chicken is being cooked in the pot. Hold it down with a small basket, lift it up frequently and handle carefully so that the chicken does not burst.

(322) *Colocasium* (Colocasium)

For the **colocasium** use pepper, cumin, rue, honey, or broth, and a little oil; when done bind with roux.

The recipes gathered in the Apicius collection could be easily used to taro. Taro is used to bulk up soup and in Egypt or the Caribbean it accompanies meat and vegetables.

Isidore of Seville, who is considered the last classic author, listed *colocasia* in the *Etymologies* (*Etymologiae*, also known as *Origines*). This was a book compiled at the beginning of the 7th century AD by the author using his personal collection of ancient texts. *Colocasia* is mentioned in the book on agriculture, which derives ultimately from Columella, Pliny and Palladius (Barney, 2006). In this book, *colocasia* is included in the chapter on Rural

Matters, in the section on Aromatic or Common Plants (*Orig*. 17,9,82). At the beginning of this section Isidore stated that the names of certain plants contain their explanation, but he was conscious that it was not possible to discover the etymology of every plant, as their names change with their locale (*Orig*. 17,9,1; translated by Barney, 2006).

After the Roman Empire fell and the Arabs had invaded Egypt in the 7th century AD, Islamic culture became prevalent and literature on the use of plants flourished. It is at this point that a plant known as *culcasia*, *hulcas*, *qulqas*, and *qolqas* begins to be referred to in Islamic texts. Täckholm and Drar (1941) and Portères (1960) refer to several Arabic authors who treat *qolqas* both as a food item and a medicinal plant. In the book *Medieval Cuisine of the Islamic World,* Zaouali (2007) collected medieval Islamic food recipes, including *sitt al-shana*, a recipe for taro originally present in *The Treasure of Useful Advice for the Composition of a Varied Table* written by Kanz al-Fawaid fi tanwi al-mawa'i. The latter book was probably compiled in Egypt in the 13th century AD, and contains 37 recipes (Zaouali, 2007). The *sitt al-shana* (the lady of loathsomeness) is a dish prepared with meat, *qolqas*, and tahina (a paste made of hazelnuts, ground hulled sesame seeds and oil, green coriander and pepper). According to Portères (1960), Abu Haneefa, the author of the *Book of Plants* refers to *qolqas* as both a food and a medicinal plant.

Not mentioned in previous discussions of the history of taro in the Mediterranean world is the work of the medieval author Matteo Silvatico, and

the garden known as Giardino della Minerva (Minerva's Garden) in Salerno (Italy). Silvatico was a medieval doctor whose interest in plants led him to establish a terraced garden, which he built in the 14th century AD around the medieval walls of Salerno. This was an early example of a historical botanical garden, and has been maintained as a living botanical collection continuously, despite changes in ownership and function. In Italian, this type of garden is also referred to as a *Giardino dei semplici,* where *semplici* (in English, "simple") is the medicament extracted from one herb as opposed to a compound of herbal extracts mixed by the apothecary or doctor. The *Giardino dei semplici* represents an experimental space where the medical properties of herbs can be studied.

Cultivating his plants and experimenting with their properties, Silvatico collected his knowledge in the *Opus Pandectarum Medicinae*, also known as *Pandette* (late Latin *Pandectae*, from Greek Πανδέκται, comp. of παν- «pan» "all" and δέχομαι «dechomai» "accept"). This was written in 1317 and subsequently published in 1474 as an encyclopaedic work documenting the knowledge of plants known at the time. The most striking element of the *Pandette* in terms of the present discussion is Chapter 197, which is completely dedicated to taro, and introduces as synonyms the terms *culcasia*, *culcas*, *collocasia* (Greek), *hulcas* (Arabic), and *caso* (Latin), which Silvatico states was present in his garden:

> And I possess it in Salerno in my garden next to a beautiful fountain, and in vulgar *culcasia* is called *caso*, whose leaves filled with water like vases, delight the mind of the sick and convalescent and also stimulate minds to lust. (Translation by the author)

This text contains an invaluable source of information that has not as far as I am aware been studied by other scholars. Essentially, it is a document that enables us to link descriptions of taro in the Classic period, the Islamic world and the beginning of the Renaissance in Italy. In collecting previous scholars' knowledge on plants, Silvatico mentions individuals who had written about *colocasia* in their works. His work does not pretend to be a commentary, but more of a collection of all the information known about plants. While another Italian translation is already available (Venturi Ferriolo, 1995), a new one from Latin to English is presented here, following the text of the Venetian print-edition of 1488 (Matthaeus Silvaticus, *Liber Pandectarum Medicinae*, Venetia: Marinus Saracenus, f. 77). Chapter 197 is presented in full:

> Chapter 197
>
> *Culcasia, culcas* or *collocasia* in Greek, *hulcas* in Arabic, indeed *caso* in Latin. Pliny, in a chapter on *Culcasia*'s virtues: *Culcasia*, that somebody calls *cyamos*: the most famous in Egypt, they reap it from the Nile, with the stalk that once cooked, when is chewed it is thready, but it has a handsome thyrse that stands among the leaves that are very broad, even when they are compared with those of the trees, like those which we call in our region *Personata* (they are called *Lappago Maior* in accordance with Dioscorides) and so much are they pleased with the virtues of their Nile plant that they consider it very attractive to drink from the leaves of the *colocasia* intertwined in various shapes of vessels, etc.[In *Pandette*, Pliny's text is quoted with some errors: the correct one is translated here.]This is the herb that Dioscorides calls *faba egyptiaca*: you will find the

properties and the virtues of this plant in accordance with him under the term *faba egyptiaca*; and Avicenna calls *hulcas* this *faba egyptiaca*, about which he writes a chapter in the second book of the Canon [The Canon of Medicine]. Indeed *culcasia* is very well known in Egypt among the merchants who trade in Syria. And I have the plant itself in Salerno in my garden near a beautiful spring: *culcasia*, which in our common language is called *caso*. The leaves of this plant, full of water like vessels, delight the minds of the ill and the convalescent, and indeed excite the libido.

Serapion, in the Book of Aggregations [*Liber Aggregatus*], in the chapter on *Hulcas*, based on the authority of Galen: *Hulcas* i.e. *culcasia*. This plant has a very acrid and sharp taste and it is not very astringent. And its virtue is hot at the second degree and, once cooked, helps the stomach. And the same based on the authority of Aben Mesuay: *Culcasia* is hot and humid and increases the sperm and the root is cooked and has a good taste; it is good for the stomach and provokes appetite and urine. It is hot and humid and increases the sperm. This plant is very familiar to the Egyptians and springs up near the water, and it has large and big leaves and the root once cooked and eaten increases the body. Paulus in the chapter about *culcasia*: *Culcasia* is a plant known by everyone. It springs up near the water; its root once cooked and eaten is very useful to the stomach. Isaac in the *Particular Treatments* in the chapter about *culcasia*: *Culcasia* is a plant that springs up mostly in Egypt and it is slightly bitter and pungent whence it is hot and humid. The root of this plant, once stewed, gives off an acrid juice; and the viscosity that before was hidden becomes visible. And for this reason it produces strong and immature nourishment, but with its bitterness supports the stomach and constipates the belly. However, if they eat it moderately, it is good nourishment; and it is good for people who suffer from dysentery given its viscosity and bitterness.

Avicenna, Book II, chapter *Hulcas or culcasia*: It is a plant which bears similarity with the *alisnet* [a plant not yet identified]. It is hot and dry at the first degree; and it is salty and astringent; and its parts are not similar; and it gives little flatulence. Gargles are made with its same milk and salt; and in Egypt it is cooked with meat; and it is fried with oil; for them it is food; and mashed it releases yellow water and properly its seed and its juice, and so what debilitates is decreased; it causes urine and generates sperm and expels easily gall and water; drink from 1/3 to 2/3 of 1 lb of it."

(Translated for the author by Giulia Tozzi, doctoral student in Classics at the University of Padua, Italy and Antonino Nastasi, doctoral student in Humanities at University "G. D'Annunzio" of Chieti, Italy)

Silvatico also mentions Pliny and Dioscorides and their reference to *cyamos* or the *Egyptian bean* (see discussion above), then mentions Avicenna, Paul of Aegina, Israel Isaac, Aben Mesuay and Serapion. These authors are introduced below.

Avicenna is the Latinised name of Abū ʿAlī al-Ḥusayn ibn ʿAbd Allāh ibn Sīnā, also simply known as Ibn Sina, who was one of the most prominent philosophers in the Islamic world. He was born in 980 AD in Afshana, a small town outside Bukhara, modern Uzbekistan (Goodman, 2006), and inclined towards medicine and philosophy from an early age. He wrote a medical compendium, known as the *Canon of Medicine*, which became the main reference on medicine for centuries. Matteo Silvatico refers us to a chapter on *hulcas* written by Ibn Sina in Book II of the *Canon*, which was not discussed by Täckholm and Drar (1941), or Portères (1960). For Ibn Sina, *hulcas* is a plant used both for medicinal purposes and as a food, and resembles a plant known as *alisnet*, which remains unknown to the present author. However, the present widespread linguistic association of *qolqas* suggests that the plant in question was taro, and that the original Greek word κολοκάσια underwent phonological changes by being adopted into Arabic. The Latin word *caso*, which Silvatico suggests is the vernacular name for taro, is only present in this text (Silvatico, 1474), attesting to everyday use of the plant in addition to its medicinal use.

In Silvatico's text, *hulcas* was said to be well known in Egypt among merchants who used to travel to Syria, which might suggest that the plant originally came from that country. This reference returns in Serapion's *Liber aggregatus in medicinis simplicibus*, a text traditionally attributed to Serapion the Younger, but later identified as the *Kitāb al-Adwiya al-mufrada* (*Book on Simple Drugs*) by Ibn Wāfid (1067 AD) in the Latin translation made by Simon of Genoa (Jones, 2008). Serapion, or Ibn Wāfid, was a physician and pharmacologist from Toledo ca. 1290, who had collected and translated the medicinal texts of Dioscorides and Galen, a common practice at that time. *Liber aggregatus*, as it is also known, was listed in the *Compendium aromatariorum* (by Saladino Ferro D'Ascoli, personal physician to the Prince of Taranto Giovanni Antonio del Balzo Orsini, 1386/93-1463), a book which was required reading for all apothecaries (Jones, 2008). An illuminated copy of the *Liber de Simplicibus* was made by Niccolò Roccabonella between 1445 and 1448 (*Liber De Simplicibus*, 1419, Venezia, Marc. Lat. VI 59 [=2548]), and offered as a botanical text to his son who was about to become a doctor (Pitacco, 2002). It contains an extraordinary collection of plant drawings made by Andrea Amadio, with each drawing being accompanied by a brief description compiled by Roccabonella. After examining many of the oldest illuminated European herbaria, the present author concludes that this book may contain the oldest image of taro (Figure 73). The plant has no inflorescence but shows large green leaves and a large underground corm, and despite inaccuracy in

the leaf shape, the drawing overall displays other traits of taro very clearly.

Like Silvatico (1474), Roccabonella reports the names of the plant in Greek, Latin and Arabic, among which only *Syrian bean* (*Faba Sira*) is mentioned for the first time. The text is written in Medieval Latin handwriting and the Latin text with an English translation is reported here:

De culcasia. Capitulum 114.

Herba picta in hac carta infra scriptis appellatur nominibus.

Graece	***Latine***	***Arabice***
Faba	*Colocasia*	*Culcas*
Faba Sira		*Culcasia*
Ciamon		*Hulcas*

In medicinis utimur herba et suco eius et radice. Colligi potest tam herba et exprimi sucusquam radix, a mense Iunii usque ad finem Septembrem, quamquam herba melius de mense Iunii et radixmensem Septembrem, luna crescente. Servari potest per annum, quamquam recens melioris sit operationis. De ea tractat Serapio libro suo de Simplicibus, capitulo de hulcas, idest culcasia. Et Avicenna secundo canone, capitulo de culcasia. Et Simon Ianuensis et Mundinus in suis Sinonimis, capitis de culcas, et de hulcas, et de ciamon, et de colocasia, et de faba Egipciaca. Et Galenus librode alimentis.

(Niccolò Roccabonella, *Liber de Simplicibus*, Marc. Lat. VI 59 (=2548), 114v)

Culcasia. Chapter 114.

The herb drawn in this page is called by the following names:

Greek	**Latin**	**Arabic**
Egyptian bean	*Colocasia*	*Culcas*
Syrian bean		*Culcasia*
Ciamon		*Hulcas*

In medicine we use the herb and its juice and root. It is possible to gather both the herb, and to squeeze out the juice from it, and the root from the month of June until the end of September, although it is better to collect the herb from the month of June and the

> root in the month of September, during the waxing moon. It can be kept for one year, even though the fresh variety is preferable. Serapion treats it in his book "de Simplicibus", in the chapter on *Hulcas*, i.e. *culcasia*. And Avicenna writes about it in the second book of the Canon, in the chapter on *Culcasia*. And Simon of Genoa and Mundinus in the *Synonyms* in chapters about *culcas*, *hulcas*, *cyamon*, *colocasia*, and the Egyptian bean. And it is mentioned by Galen too in his book "On the Properties of Foodstuffs". (Translation made by the author)

In this text, Roccabonella stresses the medicinal use of this plant more than its use as food, and it gives interesting hints on harvesting periods and the way taro was stored during that time. This text is also important, as two other authors are mentioned who have never been noted before in regards to taro. The first one is Simon of Genoa, who was a medical attendant to Pope Nicholas IV (1288-1292). He built the giardino dei semplici (garden of the simples) in the Vatican residence in Rome where he studied the properties of herbs (Vatican, 2013). In 1296, he wrote the *Synonima Medicinae* (*Synonyms*), also known as the *Clavis Sanationis* (*Key of Health*), which is one the most important historical dictionaries of medicine (Steinschneider, 1892). The other author is Mundinus de Forojulio, known also as Mundinus Friulensis and Mondino da Cividale (ca. 1275-1340), who in 1321 summarised the *Synonyms* in epitomes, which, containing 6500 titles was difficult to use (Gianni, 2011). Simon is said to have been the material source for Matteo Silvatico (Mowat, 1887: v), who had included other sources in the *Pandette* that were not present in the *Clavis Sanationis*.

Figure 73. Drawing of *culcasia* made by Andrea Amadio in Niccolò Roccabonella, *Liber de Simplicibus*, Marc. Lat. VI 59 (=2548), 114r (su concessione del Ministero dei Beni e le Attività Culturali – Biblioteca Nazionale Marciana. Divieto di Riproduzione).

The next author cited in Silvatico's *Pandette* is Paul of Aegina, one of the last of the Greek physicians. He was born in Greece on the island of

Aegina in 625 AD, and practised in Alexandria (Gurunluoglu and Gurunluoglu, 2003). The passage by Paul of Aegina, cited by Silvatico, is not found in the *Seven Books on Medicine*, which is the only work of his that has survived. In this book, there is only a reference to the *Egyptian bean* (κύαμος Αἰγύπτιος), which does not correspond to Silvatico's description of *culcasia*. Part of Paul's text may be missing, or there may be other texts by Paul that are missing, as it seems unlikely that Silvatico would have inserted a text and inaccurately attributed it to Paul. Indeed, Paul of Aegina is reported, based on comments from later Syriac and Arab authors who took great interest in his work, to have written the following treatises: the *Therapy of Pregnant Women*, *On Uroscopy*, *On Lethal Poisons*, and *the Therapy of Children*, none of which have survived (Éloïse Lemay, doctoral student in Indo-European Studies, University of California Los Angeles, pers. comm.). Thus, like the other works, Paul's reference to *culcas* is present today only as a secondary source, but the mention of the *Egyptian bean* in his surviving text indicates that during the 7th century AD, these two names were used for two different plants. Moreover, according to Paul, *culcas* was 'known by everyone', which implies that it must have been around for a longer time.

For Aben Mesuay, whose original Arabic name was Yahanna ibn Masawaih, *culcasia* was also a medicinal and food plant well known to the Egyptians (Silvatico, 1474). Aben Mesuay was born in Gondishapur in the Persian Gulf in 777 AD who later became director of a hospital in Baghdad

(Shoja, 2007).

Finally, another author who has not been noticed by later scholars is Isaac ben Solomon Israeli, a physician who lived in Egypt ca. 855–955 AD. As a doctor, he wrote numerous treatises among which Silvatico refers us to *Diaetae Particulares*, which includes a chapter on *culcasia*. *Culcasia* is once again treated as a medicinal plant that was thought to be good for the stomach if eaten in moderation. This passage is also reported by Bartholomaeus Mini de Senis (i.e. "of Siena") in the *Tractatus de herbis* (*Herbal*) written around the 1310 (Ventura, 2009). The original manuscript (London, British Library, Ms. Egerton 747) is an illuminated herbarium, but it does not contain a representation of taro.

Silvatico's account is an invaluable historical resource, revealing an extensive knowledge of taro in both the Byzantine and Islamic worlds. His work provides precious hints on the uses and terminology applied to taro in Latin, Greek and Arabic. The plant he describes in the *Pandette* is still growing in the Garden of Minerva and occupies a central position in the garden (Figure 74). The terraced irrigation system of the garden is composed of the original Arabic ditches which were restored in 2001, with taro thriving in pools - the waters of which come from a natural spring. At the top of the pool there is an image of the Gorgon that was represented on the shields of the goddess Minerva, hence the naming of the garden. Minerva is the Latinised version of the Greek goddess Athena. Even though there is no known

historical connection between the 14th century AD "Giardino della Minerva" in Salerno and the 3rd century BC temple in Sikyon (Greece) that was dedicated to Athena Kolokasia (see discussion above), the goddess Athena is thus associated with *colocasia* in both locations, suggesting the incorporation of this plant not only into culinary and medicinal practice, but also in the Mediterranean religion and symbolism.

Figure 74. Taro plants growing in a fountain bearing an image of the Gorgon in the "Giardino della Minerva" in Salerno (photo by the author, August 2013).

OUINGON

Some authors have argued that the term *ouïngon*, used by Theophrastus in his *Historia Plantarum*, refers to *Colocasia esculenta*. This comes from Daniel Heinsius's reading (1613) of the text of Theophrastus following Gaza's Latin translation (Sharples, 1995), which then becomes *oetum* in Pliny (*NH* 21,88). This belief has been assimilated to the point that in the Greek

Lexicon *ouïngon* is defined as *Colocasia antiquorum* (Liddell et al., 1940). Theophrastus refers to *ouïngon* as a plant known in Egypt that bears its fruits underground (*HP* 1,1,7) that are not regarded as roots (*HP* 1,6,9), and with large leaves and long edible tubers that men gather from the Nile when the river retreats (*HP* 1,6,11). While Amigues (2010) accepts this as a description of taro, Täckholm and Drar (1941) considered this to be an unidentified plant with characteristics that differ from those of *qolqas*. Pliny's *oetum* is a plant with a big root, but with only a few small leaves (*NH* 21,88), which is enough to rule out taro, a plant bearing numerous large and broad leaves. The description of the plant and its method of harvesting given by Theophrastus could apply to either taro or lotus. Further philological research may shed more light on this topic.

ARON

An alternative view is that during Roman times taro was known as *aron* or *arum* (Anguillara, 1561; Cesalpino, 1583; Colonna, 1616; Täckholm and Drar, 1941; Dalby, 2003; André, 2010). *Arum*, or its original Greek form ἄρον, is an old term from which the plant family Araceae and genus *Arum* take their names. The *Corpus Hippocraticum* (4th-5th century BC) is a collection of medical works written in the style of Hippocrates, but is likely to have been composed by several authors; it refers to *arum* as a medicinal plant used to cure severe inflammation of the lungs (*Morb*. 2,47; 3,15-16), and as an application to

soothe burns (*Ulc*. 12,16,22). In one case, use of the root of the *arum* "large as an ossicle" (*Morb*. 2,47) is recommended, and in other cases use of the root of the "big *arum*" is suggested instead (*Morb*. 3,1-16). The difference could be related to different stages of growth of the same plant, or to the existence of two different kind of *arum*. In an early and still highly influential translation and commentary of the *Corpus Hippocraticum*, Adams (1849) interpreted *arum* as a wild *arum*. Littré (1839) considered it to be *Arum Colocasia* (an old botanical name for *Colocasia esculenta*), and in a later edition he suggested that Fraas' (1845) interpretation of it as *Arum italicum* was dubious (Littré, 1851). More recently, *Arum maculatum* L., *Arum italicum* L., and *Colocasia esculenta* (L.) Schott, have all been proposed as candidates for the arum discussed in the *Corpus* (Aliotta et al., 2003).

Aristotle (4th century BC) in the *Inquiries on Animals* (*Historia Animalium*) referred to *aron* as a root eaten by bears after hibernation to open up the stomach, which was argued to have become constricted after little or no food for so long (*HA*611b). This suggests a plant present as part of the natural flora. Theophrastus (4th century BC) provides a more comprehensive description of *arum*. In the *Enquiry into Plants*, Theophrastus described the root of the *arum* as fleshy (*HP* 1,6,7), stout and fibrous (*HP* 1,6,8), smooth loose and soft throughout and without bark (*HP* 7,9,4). Interestingly, Theophrastus also mentioned an *edible arum* whose leaves are big (*HP* 7,13,1-2), and that once both are boiled in vinegar become sweet and are good for fractures (*HP*

7,12,2). The *edible arum* is also said to have no stem or flower (*HP* 7,13,2), which might refer to taro under cultivation, since wild arum or wild (naturalised) taro can easily flower (Matthews, 2006).

A recent review of the genus *Arum* revealed that the eastern Mediterranean and the Balkans through to the Near East form the centre of greatest diversity (Bedalov and Küpfer, 2005) with a total of 28 species (Boyce, 2006). Of all the genus' species and sub varieties, none is said to be flowerless, and the notoriously poor production of flowers in some plants of taro in Africa as well as in the Mediterranean area makes taro a candidate for Theophrastus's *edible arum*.

Dioscorides (1st century AD) writes about the properties of *arum* in the *Materia Medica* (2,197):

> Aron sends out leaves similar to those of dracontium, yet smaller and less spotted; a faint purple stalk twenty centimetres long in the shape of a pestle, in which is fruit inclining to a saffron colour. The root — white like that of dracontium — is also [a vegetable] eaten boiled, and is somewhat less sharp. The leaves are preserved in salt for eating. Dried, they are boiled and eaten by themselves. The roots, seeds and leaves have the same strength as dracontium. Particularly the root, applied with bullock's dung to those troubled with gout, does them good. The root is stored in the same way as the root of dracunculum. In brief it is edible because it is not oversharp. It is also called lupha; among the Syrians it is called alimon, some call it thymon, some, dracontium, and the Cyprians call it colocassion. (Dioscor. *MM* 2,197; translation from Osbaldeston and Wood, 2000)

The reference to *colocassion* may have been added at a later time. All modern editions place the entire sentence ("οἱ μὲν ἄλυμον, οἱ δὲ θύμον ἢ καὶ

δραχοντία ἢ παρὰ τοῖς κυπρίοις κολοκάσιον λέγεται" "it is called alimon, some call it thymon, some, dracontium, and the Cyprians call it colocassion") in brackets. According to Wellmann (1907), this sentence was added later as a note in the margin of the fourteenth century manuscript *Vaticanus Palatinus Graecus* 77. The addition of the term *colocassion* to *arum* (or *aron*) is confirmed in a 16th century Italian account by Anguillara (1561) who narrates an encounter made in Cyprus between Sir Giovanni Battista Casanova and a Greek man, with whom he discussed *arum*. According to Anguillara (1561), the Greek man told Casanova that the Cypriots instead knew the plants that he called *arum* as *colocasia*. To prove what he was saying was true, the Greek man said that *colocasia* was a very old term in their language, and to further convince him he showed Casanova a Greek book of plants in which this name was present. Finally, the Greek added that the strong acridity of this plant would not allow the tubers to be eaten raw. Unfortunately, the identity of the book is unknown, as it was not specified in the text of Anguillara.

It is possible that none of the Renaissance authors had seen the *colocasia* of the ancient scholars (lotus plant); probably lotus plants were rare in Egypt and Europe. Moreover, the work of Matteo Silvatico, the *Pandette*, did not reach the wider scholarly audience, creating a discontinuity and much confusion in botanical knowledge concerning aroids and lotus.

Among others, Bartolomeo Maranta (1560), an Italian botanist of that time, raised the possibility that the *colocasia* growing in Egypt was a type of

arum. Maranta (1560) wrote that he had received a drawing of the flowers from Luca Ghini, and explained that this plant was different from other Arum plants growing in Italy. Ghini is considered to be the inventor of modern herbarium (Dröscher, 2008), and it is from him that the *Egyptian arum* began to be known as *Colocasia arum* (Pirotta, 1908). However, for Pietro Andrea Matthioli (1565) and Fabio Colonna (1616) this was not the *colocasia* of ancient peoples. Matthioli, who brought back to light the *Materia Medica* of Dioscorides (1544), had heard about the story that Anguillara reported (Matthioli, 1565) and in the 1565 edition of the *Discorsi* he included a sketch of the plant that had been brought from Egypt by his friend Augier de Busbecq (Alpini, 1735). Matthioli never went to Egypt, and learned about these plants from Greek and Latin authors who had applied the term *colocasia* to the *Egyptian bean*, so he considered that the latter was just a larger type of *arum*. However, while discussing the *Aro d'Egitto* (*Arum of Egypt*), Matthioli reported the name *colocasia* as a term used for corms. The plant provided by Augier de Busbecq and depicted by Matthioli, despite the absence of inflorescence, strongly resembles taro overall, and is very different from lotus (Figure 75).

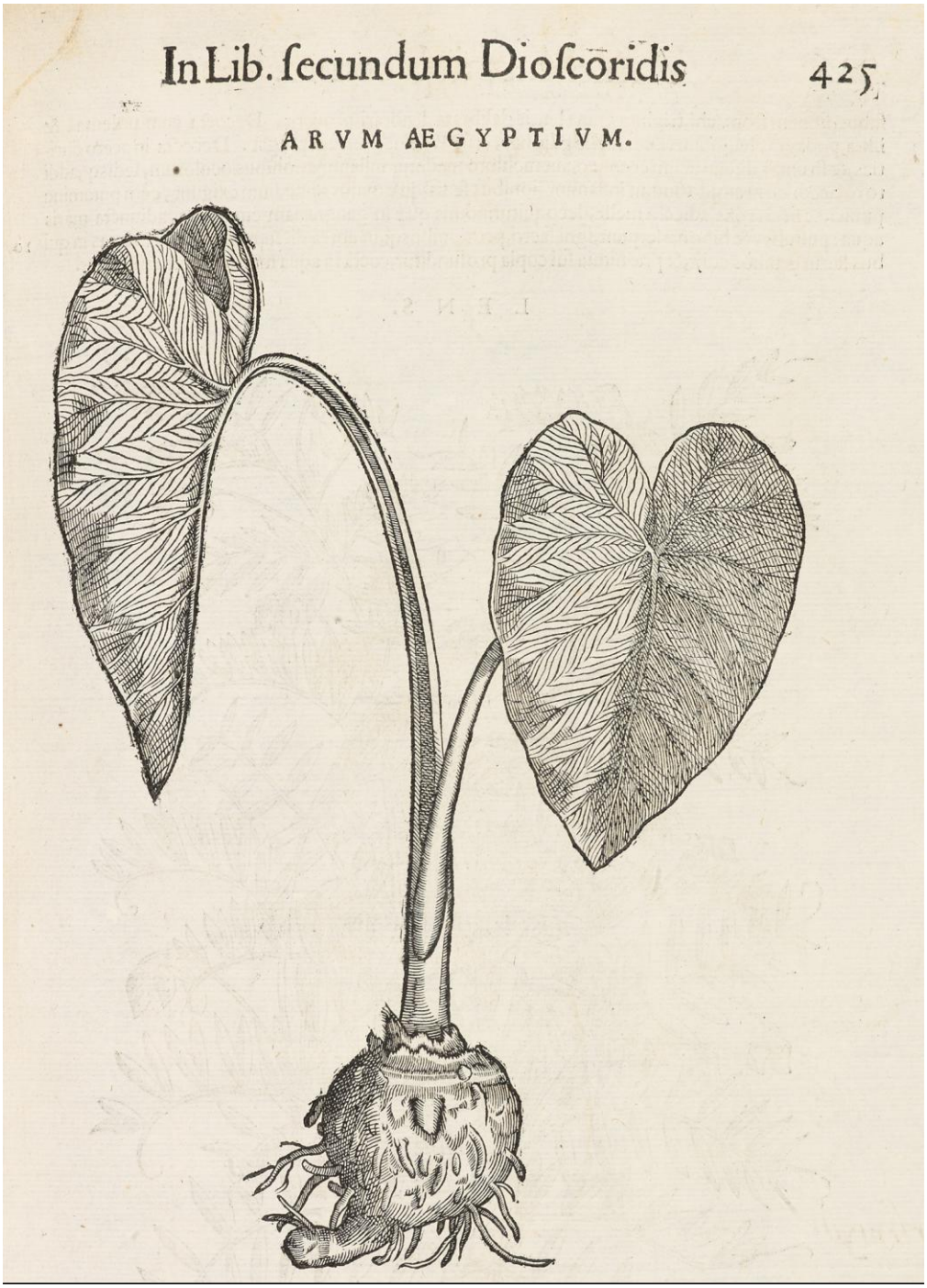


Figure 75. ***Arum Aegyptium*** **in Matthioli's Discorsi (1565). Courtesy of the Sherardian Library of Plant Taxonomy, one of the Bodleian Libraries of the University of Oxford.**

Following the modern annotation of Dioscorides' description of *arum*, discussion by other Italian scholars of the *Egyptian bean*, *colocasia* and the

Egyptian Arum continued unabated, and confusion about these names grew exponentially.

Another prominent botanist who discussed the *culcasia-Arum Aegyptium* is Prospero Alpini, an Italian physicist and botanist who had lived in Egypt for three years, where he became familiar with taro so that he wrote a chapter on plants that were known as "*culcas*, also known as *colocasia*". In his book on *Egyptian plants* (1592) he included a lifelike sketch of a plant, also with no inflorescence, but clearly depicting taro. In a later edition (1735), Chapter XI is completely dedicated to the "The roots that the compatriots (n.d. Italians) call *colocasia* and the Egyptians, who know it by *culcas*, eat cooked". While in Egypt, Alpini had noticed the popularity of taro and having heard about the dispute on the *Egyptian arum*, wanted to shed light on whether this was the *Egyptian bean* of the Greeks. His arguments were mainly based on the shape of the corms. What he had seen in Egypt, known locally as *colocasia* or *culcas*, were plants with roots that were, thick, of dark skin colour in the outer part, white inside, and characterised by an acrid and astringent taste, meaning that they had to be cooked. Another type of root, of rounder shape, was also growing in Egypt, but he considered them just two variations of the same plant, as they were not distinct in taste and texture.

Finally, Alpini (1735) referred to his surprise on hearing from other scholars about what they thought was a *colocasia* plant that had bloomed in Naples. He had never seen and never heard of anyone who had seen the

flowers or fruits of this mysterious plant. Likewise, in a later edition supported by the notes of Johann Vesling, it is interesting to learn from Alpini that a plant of *culcasia* had bloomed in Italy (1735), to which he added another sketch with the inflorescence characteristic of taro. At that point, Alpini was trying to retrace the ancient scholars in an attempt to find the *Egyptian arum*, promising to continue his research in shedding light on the *colocasia*.

Renaissance authors who discussed the *colocasia-arum* dispute were also well aware of Pliny's *arum*, which led many authors to think it was indeed taro. In *Natural History*, Pliny (1st century AD) mentions *arum* several times, and on this subject the latest etymological dictionary of Greek (Beekes, 2010) offers an interesting and new interpretation of *arum* etymology, connecting it with Egyptian *r* 'reed, cane', and referring to one of Pliny's passages on *arum*:

> *Est inter genera et quod in Aegypto arum vocant, scillae proximum amplitudine, foliis lapathi, caule recto duum cubitorum, baculi crassitudine, radice mollioris naturae, quae estur et cruda.* (Plin. *NH* 19,96)

> Among the varieties of the bulb, too, there is the plant known in Egypt by the name of *aron*. In size it is very nearly as large as the squill, with a leaf like that of lapathum, and a straight stalk a couple of cubits in length, and the thickness of a walking-stick: the root of it is of a milder nature, so much so, indeed, as to admit of being eaten raw". (Translation from Bostock and Riley, 1855)

This passage on *arum* is worth considering. The first one is the Egyptian linguistic nature of the name *arum*. According to Dr Robert Simpson, Faculty of Oriental Studies, University of Oxford (pers. comm.), there is a word transliterated as *'i3rw* meaning 'reeds' or 'rushes' which he supposes one could argue to be the source of Pliny's *arum* (Figure 76).

Figure 76. Hieroglyphs for *i3rw*, whose transliteration reads as *reed, cane*.

The hieroglyphs represented in Figure 76 are present in several funerary papyri (Budge, 1906). In the papyri, there is a place known as Sekhet-Hetep, "Field of Peace", rectangular in shape, and intersected by canals (Perry, 1912) where the righteous dead would enjoy a fertile land with running streams. Sekhet-Aaru, literally "Fields of Reed Plants", was said to be a section of it, a place where constant and abundant supplies of wheat, barley, incense, and unguents were present, "the true heaven of every faithful worshipper of Osiris" (Budge, 1906). This Earthly heaven seems to have been situated in the Delta, to which Osiris belonged (Perry, 1912), a fertile and well irrigated region where *arum Aegyptium* could have easily been cultivated since ancient times.

An association of taro and reeds would not be surprising since taro is a semi-aquatic plant often found at the margins of streams, in lakes and ponds or anywhere with abundant water (Figure 77).

Figure 77. Taro plants growing in a fountain in Tropea, Italy August 2010. Photo by the author.

The *arum* of Pliny is said to have leaves similar to the ones of the *lapathum*, a plant that is generally interpreted as the sorrel, *Rumex* sp. (Lechi, 1984), which do not resemble taro. However, a more convincing aspect suggesting that Pliny's *arum* was taro is the comparison of the roots of squill, *Drimia maritima* (L.) Stearn (Lechi, 1984), with those of taro (compare Figure

73 and Figure 78). Among aroids present in the Mediterranean and Near-East region, none has a corm the same size as squill except taro.

Figure 78. Corm of *Drimia maritima* (L.) Stearn. Photo by the author, Rome, August, 2013.

Galen (2nd century AD), in his work *On the Properties of Foodstuff* (3,61), writes about two types of *arum*, one that is used primarily for medicinal purposes and which is found in Greece, and a second that is cultivated in Cyrene (near present Shahhat, Libya) and used for food, and also traded in Italy.

> The root of this plant is eaten much the same as that of the turnip, but in certain regions it grows somewhat more bitter; so that it is very like the root of the dracunculus [translated as edder-wort]. In cooking, one should pour off its first water and add more hot water, as was described in the case of cabbage and lentils. But in Cyrene the plant is the reverse of what it is in our country. For in those parts the arum has very little pharmacological activity and very little bitterness, so that it is more useful than turnips.

> Because of this they also export the root to Italy, on the grounds that it can keep for a very long time without rotting or sprouting. It is clear that this sort is better as nutriment, but if one wants to cough up any of the thick, viscid, fluids that accumulate in the chest and lung, the more bitter and more pharmacologically active root is better.
>
> When boiled in water, it is eaten with mustard or with oil, vinegar fish sauce, and of course with other mashed dishes, especially those prepared with cheese. But it is plain that the humour distributed from it to the liver and the body as a whole, from which animals are nourished, is somehow thicker, as was mentioned in the case of turnips. This is especially the case when the roots, like those from Cyrene, have no pharmacological activity. With us in Asia, many arums are more bitter and have medicinal property. (Gal. *Al. Fac.* 3,61; translation from Powell, 2003)

In Galen's passage, the medicinal plant referred to is likely to be arum or another wild aroid, while the Cyrenaic plant is presumably taro, judging by the cooking method described and its palatability.

For Pliny, there were also two different types of *arum*, one that he called *feminine* (Latin: *femina*), which is preferred for cooking to the other, which he called *masculine* (Latin: *mas*) which is harder and more time consuming to cook, and therefore used to cure chest problems if dried and sprinkled in a drink (*NH* 24,143). In Cyprus, this distinction was made with regard to different forms of taro: plants that were in the flowering phase at harvest were regarded as 'male', and produced harder corms; those that were not in the flowering phase were regarded as 'female', and produced softer corms. The difference was not recognised by reference to flowering, but by reference to the cross-section of cut petioles seen on corms sold in the markets.

In the cross-section, an extra circle marked the 'male' plant. Anatomically, the extra circle marks the peduncle of an inflorescence that is not seen by the buyer (Peter J. Matthews pers. comm., observation in 1996).

During the Renaissance, many authors discussed the identification of the *colocasia* referred to by the classic scholars. Bauhin lists all of them in a chapter on the *arum* inserted in the *Pinax Theatri botanici* (1623), a collection of some 6000 plants that were described in the pre-Linnaean manner. For William Turner (Britten, 1881) *colocasia*, which he said he had seen in Italy as well as in Germany, was the Egyptian bean. Clusius (1601) provides an illustration of taro, which he had seen in the monastery of Penha Longa in Portugal. For him, this was the *Egyptian Arum*, and not the *colocasia* as other authors had stated. In *De plantis libri XVI*, Andrea Cesalpino (1583) compiled all the information and descriptions of *arum* made by classic authors. Even though a detailed philological analysis shows some discrepancies between the original Greek and Latin texts and the text written by Cesalpino, an original translation from Latin into English is reported here. A standard font indicates Cesalpino's writing, whereas the parts written in italics were recognised as passages of ancient scholars recalled by Cesalpino.

Chapter *ARON MAGNUM*

Aron magnum, which is commonly called Colocasia, sprouts in Sicily: with broad leaves, in the size (similar) to the personata [*Arctium lappa* L.], in the aspect to the Ighero [*Arum*

maculatum or *Arum italicum* L.], but with the lower corners of the leaves joined, so that a sort of concavity is formed in the leaf, with an extremely smooth surface and extremely lush, with variation in colours and resembling verdant and luxuriant waves. A thick pedicle the thickness of a walking stick, one cubit long and more, and from where a leaf that faces downwards hangs. The inhabitants [it is not clear whether Cesalpino refers to people living in Sicily, or generally in the Italian Peninsula] call them 'Pampina Paradisi' [literally 'Heaven's trumpets': this is still one of the names applied to taro in Italy]: they use the leaves to preserve fresh fruits and fresh cheese. The underground root is round and thick, like the one of the Dracunculus maior, certainly bitter, but with an innocuous taste. This does not carry a stem, nor a fruit; it becomes lush during the entire summer, it loses the leaves during the winter, and it needs abundant water. Theophrastus calls it 'aron' and 'edible aron'. He reports this information about it here and there [so far, it seems that Cesalpino has summarised his knowledge of *Colocasia esculenta* L.; from now on he refers the texts of other authors]. *The very broad leaves are scattered and they are concave and large like the ones of the Cucumeracea. There is no stem, nor a flower, the root is edible also the leaves once cooked in vinegar* [cfr. Theophr. *HP* 7,13,1-2]. *It is agreeable to the taste, and good for fractures. The root is soft throughout, almost without skin, and it is fleshy. It has another root thin and with tough fibres, such as to doubt whether to call them 'root' as also in the Cyperus. When the root is thriving with the leaves, to increase the growth the inhabitants use to cover it all around, bending the leaves themselves, so that the plant does not grow on their buds, but drag all the nutriment on its head* [cfr. Theophr. *HP* 1,6,8-10][This is a very precise description of how taro is commonly managed towards the end of the growing period, in Asia and the Pacific generally (Matthews, pers. comm.)]. *Pliny talking about the aron similarly considers this edible, and it is in great controversy with the dracontium* [*Dracunculus vulgaris* Schott]. *Some said that they are the same thing. Glaucias distinguished them from the place of growth, calling dracontium the wild arum. Others call the root aron, the stem dracontium, which is completely different. The root of the arum is black, broad and round even much bigger so that it fills the hand, much revered both as food and as medicament. It is said that cheese is best kept in the leaves of arum* [cfr. Plin. *NH* 24,142-148]. *Among the different types of bulbs in Egypt there is the one that they call arum, similar in size to the scyllae* [squill (*Drimia maritima* (L.) Stearn)], *and for the leaves to the lapathum* [sorrel (*Rumex acetosa* L.)]. *The stem is straight, with the thickness of a walking stick of two cubits long, with a soft root, which is edible even eaten raw* [cfr. Plin. *NH* 19,96]. But we have not seen this Egyptian type (of arum) yet. For this reason, it can be inferred that Dioscorides's manuscripts are corrupted, because many things that are suitable to the edible arum, are instead attributed to the dracontium minor, like these ones: *cheese wrapped in the leaves is*

preserved from rotting. The root, either cooked or raw, is used as a vegetable for the health. In the Balearic Islands they offer the root cooked with a lot of honey in banquets instead of cakes [cfr. Dioscor. *MM* 2,197]. And some things that are suitable to the dracontium minor are attributed to the aron, like the saffron coloured fruits. However, among other names, in Dioscorides is said that Cypriots call it Colocasion, a name that is still maintained among us, even though it is confused with the Egyptian bean that Pliny says that it is called Colocasia. (Translated for the author by Giulia Tozzi, doctoral student in Classic studies at the University of Padua, Italy and Antonino Nastasi, doctoral student in Humanities at University "G. D'Annunzio" of Chieti, Italy, with the participation of the author)

The use of certain toxic aroids as food is still common in some places where people have retained old traditions and habits. In Turkey, fresh or dried parts of *Arum italicum* L. are used as both food and medicine. In particular, tubers and dried fruits are used to treat rheumatism and haemorrhoids, while the leaves are consumed as food (Salik et al., 2002). However, plants belonging to the genus *Arum* have small corms, and the very strong acridity does not allow the corm to be eaten raw.

The later taxonomic history of taro is better known. When Linnaeus compiled the *Species Plantarum* in 1753, he described taro as being based on two specimens, one that had been collected in the Mediterranean, and the other collected in Barbados. He firstly established the genus *Arum*, then described each of them as separate species. One he called *Arum Colocasia*, which encompassed what was described earlier by Bauhin (1603) as the "*major Arum that people call Colocasia*" (*Arum maximum Aegyptium quod vulgo Colocasia*), the *Egyptian arum* (*Arum Aegypticum*), and *Colocasia*, the distribution

of which was identified as Crete, Cyprus, Syria and Egypt. The second species he established was *Arum esculentum* (previously described also as *Arum minus, nymphae folio, esculentum* and *Brassica Brasiliana, foliis nymphaeae*), which was from Barbados. Linnaeus must have seen a significant difference between the two specimens, but this is not made clear in his description.

Later, Schott (1832) created the genus *Colocasia* under which he merged the two species previously described by Linnaeus and changed their names to *Colocasia antiquorum* – meaning "*Colocasia of the ancients*" – and *Colocasia esculenta*. However, Schott subsequently reduced these to *Colocasia antiquorum* Schott (1856). This name was used until the International Rules of Botanical Nomenclature (from 2011 known as The International Code of Nomenclature for Algae, Fungi, and Plants ICN) were established at the beginning of the twentieth century. According to this code, a species with a valid specific name that had previously been established in a genus (genus *Colocasia*, specific name *esculenta*), cannot be reduced to a variety rank. Since the specific name *antiquorum* was created later, this latter is an invalid name and had to be reduced to the variety rank (Hill, 1939). Nevertheless, it is still not uncommon to find articles in which the invalid *Colocasia antiquorum* erroneously persists.

CONCLUSIONS

The presence of taro (*Colocasia esculenta* (L.) Schott) in the Mediterranean has been surrounded by a convoluted linguistic debate

concerning the origins and meanings of names for the plant and the period of introduction of the plant in the area. In different countries, many different local names are applied to the plant, but as in ancient food crops, its taxonomy is quite confused. In the English-speaking world, this crop is mostly known as taro. Linguistic evidence indicates the use of κολοκάσια and *arum* as names for taro in antiquity in the Mediterranean "Old World". Here, a more comprehensive investigation on these two terms has been outlined. These ancient names are present in early Greek, Latin, and Arabic literature, but were often confused by scholars with other edible root crops, or had vernacular meanings that were not restricted to taro. Since antiquity, it appears that *arum* has been used as generic term for aroids native in the Mediterranean region, and used as food plants or for medicinal purposes. It is not known when taro first came to be known as *arum*, or as a member of the *arum* group. *Colocasia*, a name of likely Sanskrit origin, may have had a generic use as a name for edible roots, including the rhizomes of Indian lotus, *Nelumbo nucifera*, as well as being a name for taro. The descriptions applied to *colocasia* suggest that from ca. 2nd century AD onwards this name stopped being applied to the roots of the Egyptian bean, *Nelumbo nucifera*, and became the name for taro *Colocasia esculenta*.

The present distribution of taro (Figure 71) reflects a long history of use, trade, and dispersal of the plant among diverse peoples of the Mediterranean rim. Accordingly, there has been ample time for further movement of taro

from the Mediterranean region into Sub-Saharan Africa. This topic is considered further in Chapter 7.

Taro, which is not native to the Mediterranean and was certainly introduced from its Asian native area, arrived at some point in the Mediterranean region, although it could have been known under a different name or changed its original name while being moved around by people from different regions. In the *Pandette*, the encyclopaedic work written in the 14th century AD by Matteo Silvatico, it seems that taro was most commonly known as *culcasia*, *collocasia*, *caso* and *hulcas.* Whether its original Egyptian name was *arum*, a term that may be connected to the transliteration of Egyptian hieroglyphs for 'reed', is a new suggestion that requires more detailed investigation by philologists. After more than 2000 years, these names were reunited and assigned to examples of taro that were growing in Egypt and in Italy. In the 16th century, taro started to be known first as *Egyptian Arum*, *Arum maximum quod vulgo Colocasia vocant* (Matthioli, 1583; Cesalpino, 1583; Pirotta, 1908), until Linnaeus created the genus *Arum* in which he inscribed, among others, the species *Arum colocasia* for taro plants growing in the Mediterranean rim, and *Arum esculentum* for those plants collected at Barbados (1753). Later, Schott (1832) renamed the two species, which he eventually inscribed in the genus *Colocasia*.

CHAPTER 7 DISCUSSION

The Mediterranean Sea, Red Sea, and Indian Ocean are three bodies of water that have been important for the movement, since ancient times, of people and materials into and around Africa. The present work on taro, while only a first step towards a more comprehensive account of the history of the domestication and spread of the plant, has nonetheless offered insights into the movement of taro between Asia, the Mediterranean world and Africa. In light of the results obtained, I will in this discussion first consider the connections that have existed between the Indian Ocean and Africa in antiquity, and secondly explore the role that the Mediterranean Sea played in connecting people. I will then discuss the genetic results obtained from the analysis of taro plant material collected in Africa and elsewhere. Ethnobotanical observations of taro collected in Africa will be integrated into the historical discussion. An assessment of the three hypotheses previously advanced for the introduction of taro will be undertake in light of the study findings, and a tentative scenario for the introduction of taro to Africa will be proposed.

HISTORICAL MARITIME CONNECTIONS IN THE INDIAN OCEAN

Although early modern humans may have first left Africa some 60,000 or more years ago by land via the Nile and the Levant, it has also been suggested that a sea crossing was undertaken across the Bab al Mandab Strait, which links the Horn of Africa and the Arabian Peninsula (Beyin, 2006; Oppenheimer, 2009). Crossing of the open ocean was certainly necessary in the subsequent colonisation of Australia by 45,000 years ago (O'Connell and Allen, 2004). These sea crossings may have marked the beginnings of a seagoing tradition, which thousands of years later would come to link up the entire Indian Ocean world (Pearson, 2008; Chaudhuri, 1985). Indeed, the Indian Ocean was the first ocean that connected distant lands, people and culture in interlinking maritime exchanges (Mitchell, 2005: 99).

The beginning of long distance trading in the Indian Ocean appears to coincide with the emergence of more complex societies in the Nile valley, Mesopotamia, and the Indus Civilisation (Pakistan), from ca. 3000 BC onwards (Boivin and Fuller, 2009). By the late Bronze Age, contacts across the eastern Mediterranean had begun to directly link up Egypt and Mesopotamia (Mark, 1998 in Ray, 2003: 84). Trade networks in the Old World expanded further in the Classical period, beginning in Hellenistic times and accelerating further in Roman times, particularly as a result of the opening up of the

monsoon-driven, direct route between the Red Sea (linking up ultimately to the Mediterranean world) and southern India (Casson, 1989; Ray, 2003; Tomber, 2008). By the Medieval period, the Indian Ocean was regularly traversed by sailors from different places, with increasingly intense interaction driven by the emergence of a shared Muslim tradition in many regions (Chaudhuri, 1985).

Africa was in contact with the Indian Ocean world via both Arab land and sea trading routes, and a less well understood link to Southeast Asia. This Southeast Asian axis of interaction ultimately resulted in the colonisation of Madagascar by Austronesian-speaking peoples, sometime in the 7th/8th century AD (Adelaar, 2009). Human genetics has contributed to the investigation of the westward Austronesian expansion, and offered strong support for linguistic data, while also revealing shared African ancestry in Madagascar, highlighting the synergy of an interdisciplinary research (Ricaut et al., 2009; Tofanelli et al., 2009).

Two key routes from Asia may be implied for the dispersal of taro to Africa. One would have involved a coastal (and probably partially land-based) route, and the other a more direct sea route, probably in association with the westward Austronesian expansion or subsequent trading activities. Some evidence in terms of which route was taken may be drawn from the fact that the name for taro in Madagascar is considered to be of Austronesian origin (Täckholm and Drar, 1941: 378-379). However, contrary to this opinion

is Beaujard (2011), who, based on linguistic evidence, has proposed that the first Austronesian arrivals on Madagascar brought rice with them (*Oryza sativa* L.), the greater yam (*Dioscorea alata* L.), the coconut tree (*Cocos nucifera* L.) and Indian saffron (*Curcuma domestica* Val.). He argues that taro only arrived later. The word for taro, *sonjo* or *sauna* could be associated to *soñga* (KiPemba) and *ncõnga* (KiGuny) in the Swahili languages (Sacleux, 1939 in Beaujard, 2011). Whether these words come from the name *m'sanga* recorded in Tanzania by Watson as a word for taro (Watson, 1983: 68), is not known. The possibility that taro in Madagascar might be a result of Swahili or Arabian influence (Watson, 1983) will be addressed later in the discussion.

GENETIC STRUCTURE AND POPULATION GENETICS OF TARO IN AFRICA

The genetic analyses performed on taro samples collected in Africa and in the countries outside of Africa may provide insights into the varying scenarios for the arrival of taro in Africa. In particular, the screening and analysis of four molecular markers in the chloroplast and nuclear DNA of taro plants provides the basis for this discussion.

The analysis of the chloroplast locus revealed a single nucleotide substitution that divides the samples into two clusters. These two groups seem to correspond with the chloroplast genotypes that were characterized by

Ahmed et al. (2012; 2013). In this study they were named *mk1* and *mk2*. The dual nature of taro chloroplast is especially evident in the multivariate analysis, and although it was conducted using only nuclear microsatellites, the results still showed that taro samples cluster into two groups (Figure 61, pag. 164). This outcome is also due to the fact that taro is a plant that is clonally propagated; however, mixed samples in both clusters suggest interbreeding between plants. In this respect, observation of flowers during fieldwork and of swollen ovaries at the same site may indicate that taro pollination occurs in Africa during the flowering period. Indeed, Figure 41 at pag 119 shows the presence of pollen in one of the two flowers observed during the African survey. Possible pollinators were observed on the leaf blade surface of a taro plant in one location, but this remains only a possibility, as association of flowers and pollen vectors was not observed.

The presence of two groups was also detected with the cluster analysis in which a 100% bootstrap value strongly supports the results obtained with the multivariate analysis and the investigation of the chloroplast region. It has to be stressed that both the cluster analysis and the multivariate analysis did not include the chloroplast information, leading therefore to an independent result. While the cluster analysis has been important in supporting the existence of two groups, on the other hand, it could not resolve the relationships within the groups of the resulting dendrogram. This result might indicate that phylogenetic events within the subgroups are still too

recent to be detected. Consequently, a higher number of molecular markers may be of help to resolve relationships within clusters.

The three nuclear microsatellite loci that were investigated were characterised in Mace and Godwin (2002), and they were used with the aim of providing a common base with which to compare the genetic composition of taro in Africa and in Asia. The loci used were Xuqtem84, Xuqtem88b and Xuqtem91. These molecular markers were found to be highly polymorphic and therefore informative.

The overall allele frequency pattern shows that taro populations outside Africa demonstrate greater diversity compared to populations of taro within Africa. This result is in line with the assertion that taro has an Asian origin. In particular, the South Asian population, identified by samples collected in India and Sri Lanka, generally shows greater genetic diversity compared to the Pacific. This supports previous results (Lebot and Aradhya, 1991; Kreike et al., 2004) in which greater diversity was found in populations of taro located in the Indonesian area compared to a more homogenous gene pool spanning taro cultivars which are cultivated on Pacific islands.

When we look at the genetic diversity of taro in Africa, this eastern influence is evident. The analysis of allele frequency of locus Xuqtem84 and locus Xuqtem91 shows that eastern Africa accounts for greater genetic diversity compared to West Africa. On the other hand, diversity in West Africa is greater when locus Xuqtem88b is observed. This locus is

characterised by a trinucleotide repeat unit (CAT)n, but the presence of another four mononucleotide repeat units could represent additional sources of nucleotide variation, and explain its higher level of heterozygosity.

The genetic analyses, and in particular the sequencing of locus Xuqtem91, have revealed that in East Africa there are taro samples that contain a mix of alleles that are present in wild plants (that were collected in India) and ordinary cultivated varieties. The resulting plants were not used for food, but were instead considered as ornamental plants, as the corms were rudimentary and characterised by a strong acridity that led people to consider them toxic. These plants were found in Kenya, along the main road at Maua, and in another location distant from any human settlement growing in a ditch alongside a rice paddy field. It was not possible to take pictures at Maua, but the plants can be described as having a dark petiole and an almost black leaf blade. The corms were of a white colour and almost non-existent. In the second case, the plants were photographed (Figure 32 and Figure 33 at pag. 115), the morphology showing a dark green petiole and dark green pointed leaf blade. The genetic results from these two types of plants imply taro breeding, likely outside Africa, and a subsequent translocation into East Africa.

An interesting result comes from the Analysis of MOlecularVAriance, AMOVA. The findings indicate that variation within taro populations accounts for 71% of the total variance, implying a considerable level of

mixture between taro plants across populations. This result is in line with fieldwork observations in which morphologically distinct plants were found at the same sampling location. This observation is paralleled in the results of the work carried out on South African taro by Van Rensburg (2011), which indicates germplasm exchange between Nigerian and South African farmers. Farmers and traders have certainly been responsible for the reshuffling of plant material. However, interviews held during the African survey and accounts in the literature (Täckholm and Drar, 1941; Winterbottom, 1803: 64) confirm that new biological material was introduced to Africa at a particular time. This will be discussed later.

ASSESSMENT OF GENETIC STRUCTURE AND AGE OF OCCUPATION ANALYSIS

The African survey was pivotal not only in the collection of plant material to be used in the genetic analyses, but also for gathering information on the historical and recent varieties present at the time of the collection, as well as for the observation of agronomic practices and ethnobotany, including medicinal uses and culinary practices. As discussed above, greater genetic diversity is generally found in East Africa than in West Africa. This result implies that taro first arrived in the east and later spread across Africa. However, new plant material was introduced during the last century to

replace old varieties characterised by an astringent taste and long cooking duration. This seems to have happened in the north of Africa (Täckholm and Drar, 1941: 382), in the east, and in the west (Dalziel, 1937; author's fieldwork observations).

The genetic structure of taro populations in Africa was investigated using STRUCTURE, a software package that uses a Bayesian approach to identify the most likely number of clusters of taro in Africa. The analyses performed with STRUCTURE indicate the presence of at least four groups (K) of taro in Africa (Figure 65 pag. 171), coloured in blue, red, yellow and red. The four (K) clusters were plotted on a map, the result highlighting the mixed composition of taro in Africa (Figure 67 pag. 174), as previously pointed out. The four groups have a high correlation with the chloroplast types, as discussed in the Chapter 5 Genetic result.

When data gathered in the field are used to analyse the clusters identified by STRUCTURE, more information can be extracted. For example, with this analysis, two groups of plants that were said to have been introduced in the last century can be distinguished: the yellow group, and the green group.

The yellow group is composed of Igbo cocoyam, a plant known to have been introduced into Cameroon in the 1940s by the Igbo tribe. This variety shows a single corm of the dasheen type, better adapted to tropical humid climates. Figure 67 at pag. 174 shows that the yellow group is present also in

Madagascar, but present work shows that this type is less frequent in Central and East Africa. This pattern could indicate that it was introduced separately in Madagascar and in West Africa, but has yet to spread across Africa. Compared to other varieties, this variety seems to have low acridity for better taste, is easy to cook, and is therefore preferred for growing. Dalziel (1937: 481), during a survey conducted in West Africa, referred to a new improved variety of taro in this region. The combination and association of the ethnobotanical observations, genetic analysis, historical reference, and distribution pattern, suggest that the plant known as *Igbo cocoyam* is a variety of taro that was introduced to West Africa in the last century and that is gradually expanding across Africa. It is less clear when this plant was introduced to Madagascar, and the present work cannot unfortunately contribute to addressing this question.

The group identified by STRUCTURE and coloured in green (Figure 67, pag. 174) was also identified by local farmers as a variety introduced after the 1940s. It is similar in appearance to the Igbo cocoyam, with dasheen-type corm morphology, and is likewise better adapted to wet climates. In Kenya, this type of plant is identified with the name *nduma ngiringaca*, grows under rain fed conditions, but always in well-watered locations at the bottom of valleys and near streams. The distribution of this plant in East Africa seems to indicate an introduction into Africa, possibly via the sea. Connections with Madagascar are evident.

As discussed earlier (Chapter 2), on Madagascar there are many names that are used for taro. Nonetheless, the present study was only able to investigate five samples of taro from Madagascar, and complete morphological descriptions of the two types were too vague to associate them to the eddoe or dasheen categories. Generally speaking, ethnobotanical observations on taro in Madagascar are too rare to frame it in the broader African picture. Further sampling and ethnobotanical research in this area would certainly improve understanding of both the history of the plant on this island, and broader questions concerning the westward Austronesian expansion.

Whether the variety *nduma ngiringaca* arrived earlier than the 1940s, the date recalled by Kenyan farmers, has yet to be confirmed. Täckholm and Drar (1941: 382) referred to a variety of taro that was introduced at that time under the name *Qolqas americani* and distributed by the Horticultural Section of the Ministry of Agriculture to the farmers of the Minufiya province in Egypt. Because of the limited sampling of taro in Egypt, in this study it was not possible to indicate whether the *nduma ngirigaca* or the *Igbo cocoyam* could be associated with the *Qolqas americani* recorded by Täckholm and Drar (1941).

If nduma ngirigaca had arrived prior to 1940, it must not have reached Kenya. It is evident from farmers' recollections, and information found in Kenyan folklore, that the local variety of taro known as mwanake was the

main type of taro grown in this region until the introduction of this improved variety.

The other two groups identified by STRUCTURE, the red and the blue, are considered (by farmers and local informants) as local varieties that have always been present. Their distribution is diametrically opposite. The red group follows a double vertical axis along the east and west side of Africa, but this group is not represented in the samples collected in the central African countries such as Burundi or eastern Congo. On the other hand, the blue group follows a horizontal direction, with an east/west gradient.

The plants that fall into the group that are red in colour are similar in morphological appearance and genetic composition at the three loci investigated. These plants are characterised by a large mother corm of a dasheen type, having a bright green petiole with a white base, pink basal ring at the bottom of the petiole and pale or yellow-tinged leaf blade. These are all typical traits of Egyptian taro (Peter J. Matthews, pers. comm.). They produce flowers very rarely, although Matthews (2006) observed them in Cyprus. They can reach up to 2m in height and are less tolerant to drier environments, so they tend to grow near watercourses or anywhere where there is abundant water for them to thrive. In this discussion, in order to refer easily to this type of taro plant, it will be referred to as the 'Mediterranean type'.

The Mediterranean type is widely cultivated in Egypt and Cyprus, and is used in local cuisine in a large variety of ways (Matthews, 2006). In

Cameroon, this plant is known as *mangua*, and it is still cultivated as a food source. In the region visited in Kenya for example, this variety is no longer eaten, though it is still left at the margins of fields in case of food scarcity. Samples belonging to this cluster are not found in Central Africa or in Madagascar. However, when dealing with the Madagascan population caution must be exercised because of the limited number of samples, which therefore may not be representative. Genetic analysis of red coloured samples shows that the plants collected in the Mediterranean have a similar composition to those of Cameroon, Kenya and North Tanzania. Their distribution in Africa suggests that they may have entered via the Nile and spread eastwards and westwards at different times through human agency. This would support the hypothesis advanced by Reinhardt (1911 in Rivers, 1926), Burkill (1935: 639) and Watson (1983: 68) of an introduction of taro in Africa via the north. The absence of taro from the Roman levels at Myos Hormos, and later presence in the Medieval period may suggest a Medieval dispersal into Africa, though not too much should be extracted from this limited dataset. Nonetheless, Watson (1983: 68) suggested that Arabic-speaking people were responsible for the translocation of taro into Africa and elsewhere in the Indian Ocean world, and the results obtained do not contradict such an interpretation.

At this point it seems useful to discuss the historical information linked to the Greek word *colocasia*. In Chapter 6, the presence and usage of this word

in Classic, Byzantine, Medieval and Renaissance texts have been reviewed. From the texts analysed, it seems that *colocasia* was a name that was originally applied to the roots of the Indian lotus plant (*Nelumbo nucifera* Gaertn.) and that at some point, probably between the 2nd and 4th century AD, it became the name for taro. In Palladius (4th century AD), the description for growing *colocasia* seems to suggest that it was taro and not lotus plant. Also, in the Apicius collection (2nd-4th century AD), the recipes for cooking *colocasia* are similar to recipes for cooking taro. Nonetheless, these sources do not provide proof of the presence of taro in the Mediterranean area. Later texts indicate that by the 7th century AD in the Mediterranean area there were two plants, one known as the *Egyptian bean* (probably the lotus plant) and the other as *culcasia*. In the past, like today, taro seems to have been considered a medicinal plant, although the scarcity of systematic studies, and the confusion of the types of taro roots used does not allow a full review of this issue.

Going back to the question of a northern introduction of taro into Africa, the absence of taro from Roman-period Myos Hormos, when it seems to have been present in the Mediterranean world requires explanation. One possibility is that the plant simply did not disperse until later to Egypt. However, it is also possible that taro was a relatively minor crop in Egypt at this time, and not grown in the arid environment of the Red Sea coast. If we take the view that taro was for a long time a minor crop in Egypt (as argued for a range of crops translocated across the Old World; Boivin et al., 2012),

then it may be that taro was present even earlier than the Roman period in this region. Nonetheless, this seems unlikely for a number of reasons, not least of which is that Täckholm and Drar (1941: 372) have pointed to the absence of depictions or full recognisable descriptions of taro during Pharaonic times. On the other hand, the preference for flowering plants is evident in Pharaonic depictions, and if the Mediterranean type of taro did not flower or only rarely, it might have attracted less attention in the artistic representation of the existing flora.

The other name that has been reviewed in this thesis is the Greek word *aron*. The Etymological dictionary reconnects this word to the Egyptian 'r', that indicates reed or cane (Beeks, 2010). It is difficult to comment on this subject as it is beyond the author's expertise, but being a new interpretation it was reported for completeness and is left to philologists to return a better assessment.

Returning to the genetic characterisation of the Mediterranean type, during the scoring of alleles, samples collected in Cameroon (Table 13 pag. 143), which fall into this cluster, showed three bands. This result raises the question of the potentially polyploid nature of taro in Africa, and further karyotyping analysis aimed at investigating this issue is strongly advocated. It might be useful to note that the corms of the Mediterranean type show intermediate characteristics with oblong shaped corms observed in the Mediterranean (Peter J. Matthews, pers. comm.; author's observation) but in

Cameroon the corms are round and large. Domestication processes cannot be ruled out, especially in light of the important cultural value that taro has in West Africa.

The question of when and how these samples arrived in West Africa still remains open. The Nile has certainly acted as a natural corridor for the spread of taro in Africa, as attested by the presence of taro in South and Central Sudan. Taro is also present in Chad (Ramsar, 2005) and Central Africa. Were these regions involved in its translocations to West Africa? In this study the lack of samples of taro from these areas does not allow this question to be addressed. Ethnobotanical and genetic study on taro in these regions might help to solve this issue.

Finally, the group identified by STRUCTURE, and identified by the colour blue, includes samples only of the mk2 type. Plants falling into this cluster usually present a dark brown petiole and a dark green leaf blade. The corm morphology indicates that they could be of the eddoe type, characterised by a central mother corm with small cormels aside. A clear distinction is made when looking at the use of plants of this group in West and East Africa. In Cameroon, the plant known as *country coco* is used for food, often mixed with other varieties of taro. In Kenya, the same plant, known as *mwanake*, is said to be very acrid and although found sporadically under cultivation, is farmed on a small scale and mainly used for medicinal purposes. The observations gathered during fieldwork indicate that this

variety is better adapted to drier conditions. Drawing upon the work carried out by Ibrar Ahmed, this plant can be assigned to a lineage of cool-adapted triploid plants, possibly of Himalayan origin (unpublished results). In this study, the distribution of the blue group tends to lie more on the eastern side of Africa, but it is also present in Cameroon. This variety, being adapted to cold environments, tends to be present in high latitude and high altitude regions of India (Kuruvilla and Singh, 1981; Yoshino, 2002), and, compared to diploid forms, is less frequently present in the Southeast Asian and Pacific region (Kreike et al., 2004; Yen and Wheeler, 1968). Its presence in Ethiopia raises the question as to whether it was introduced via the Horn of Africa, following a mixed land-sea route. In any case, an eastern introduction route for this variety is supported here.

To what extent the historical reference of al-Masudi (1864) to a plant in East Africa known as *kaladi*, also present in Yemen, is this variety remains a matter of speculation. Taro is still present in Yemen (Wood, 1997: 315), where it is known as *kurkum*, *kurn*, and *kirkir*. The description given is of dark green leaves usually 20-50 cm long, which grow wild by the sides of small slow-moving streams in the wetter parts of the escarpments from 500 to 1500m. The roots were formerly eaten in times of famine but do not seem to be used for any purpose nowadays. While the morphological description could fit with the eddoe type identified in the blue cluster, only a genetic analysis could assess its identity.

CORRELATIONS WITH GEOGRAPHICAL AREAS AND LINGUISTIC GROUPS

Taro is an English name for *Colocasia esculenta*, which derives from the Polynesian name for this plant (De Candolle, 1883). In Africa, the name taro is used as a general term in former French-speaking colonies, like the Democratic Republic of Congo or Gabon. In general, however, taro in Africa is known by many different names. Every country surveyed used a different word for it, and, surprisingly, even in countries where the same language is spoken across a large region, different groups of people would use certain names for taro and ignore others. This is particularly true of Kenya and Tanzania, countries with a shared linguistic heritage.

In Kenya taro is cultivated by the Kikuyu who know taro as *nduma*, while in Tanzania the name for taro is *magimbi or mayugwa*. The Kikuyu are an ethnic group who belong to the Bantu linguistic family, which in Kenya is spoken by 65% of the population, but restricted to just 20% of the territory. The other two linguistic families present in Kenya are the Cushitic and the Nilotic families (Central Bank of Kenya, 2008). None of these groups represents the original languages of the region, and it seems that they were introduced at different times only in the last four millennia. Cushitic belongs to the Afroasiatic family, Nilotic is part of the Nilo-Saharan family and Bantu belongs to the Niger-Kordofan.

The arrows drawn in GENECLASS2 not only detected introduction of taro from outside, but also indicated internal movements of taro germplasm. In Figure 68 pag. 177, a double pointed arrow links West Africa with the region of the Great Lakes. The crop exchange suggested might have happened in the past as well as in recent times. The Bantu might have had a role in the dispersal of varieties that were present in West Africa. Looking at the distribution pattern of different types of taro (Figure 67 pag. 174), it may be speculated that the plants involved in this movement were of the eddoe type, which is the most common variety of taro found both in West and East Africa. Other varieties cannot be excluded, and the absence of South African samples of taro does not allow for further speculation in this regard.

COMPARISON WITH AREAS OUTSIDE AFRICA

In parallel with the present study, genetic work on taro was also carried out simultaneously by Ibrar Ahmed of Massey University, New Zealand. Ahmed's work has focused on studying the phyletic relationships within the genus *Colocasia*. While his work is undergoing revision, a first comparison of selected common samples has been reported here. The analyses of the combined nuclear microsatellite and chloroplast region suggest that African taro varieties have two distinct regions of ultimate origin:

the Himalayan region (for the eddoe types) and more southerly parts of South Asia (for the dasheen types).

For each major category of cultivated taro in Africa (eddoe vs. dasheen) (var. *antiquorum* vs var. *esculenta*, in Purseglove, 1972) there could have been multiple routes and timings of entry into Africa, but broadly speaking, the results suggest that a northern route is more likely in relation to the cultivars with likely northern origin (Himalayan-East Asian), and a southern one for more southern (South-Southeast Asian) cultivars. The comparison of African taro plants with those collected in the Asian-Pacific region highlighted the presence in Africa of one particular genotype, which in the work carried out by Ahmed falls into a cluster of cool-adapted triploids of probable Himalayan origin (unpublished results). In the analysis carried out on this particular genotype, the presence of three alleles was never witnessed, however since triploids can show from one to three alleles at one locus, only a karyological investigation conducted on living plants can confirm or reject this connection. It was not possible to undertake karyological analyses on African taro plants in this study, but in other samples that belong to another type, three alleles were observed, highlighting the possibility of these plants being triploid.

The same kind of genetic approach applied here has also begun to be applied to plants such as banana, a crop that represents a key domesticate in human history (De Langhe et al., 2009; Perrier et al., 2011). The banana, as outlined previously, is an Asian plant that is now found widely in Africa, and

its translocation together with water yam and taro, which Blench (1996) called a *tropical food kit*, has been the focus of much speculation and research for scholars who have sought to use it as a proxy to trace human movements (Murdock, 1959; De Langhe et al., 2009). Considerable efforts have helped to establish that in Africa there are two different types of banana, AAA forms that are found in the East Africa and that are used for beer brewing and cooking, and plantain AAB forms that are found in West Africa. At least two separate introductions have been proposed for their arrival in Africa, and the paucity of evidence from archaeological sites in intermediate South Asian regions, may suggest ancient maritime connections (Perrier et al., 2011), though the limitations of systematic archaeobotanical study of banana, only possible through the analysis of phytoliths (and possibly starch) is a major caveat for such an interpretation.

The interdisciplinary nature of the work carried out on banana stresses the importance and the value that the combination of diverse disciplines such as archaeobotany, genetics, history, and linguists can contribute to the study of past human activities.

ASSESSMENT OF THE THREE HYPOTHESES AND LIKELY ROUTES OF TARO'S ENTRY INTO AFRICA

The results obtained in this research enable evaluation of the hypotheses that have been proposed by scholars concerning the routes by which taro was introduced into Africa. The retrieval of taro at Quseir al-Qadim (Van der Veen and Morales, 2011) sets an absolute date for the presence of taro in the continent, but this is not the case in terms of the genetic work for taro. Also, the chloroplast region examined was not variable enough to enable phylogenetic assessment, and the microsatellite regions examined showed mixed features meaning that it was not possible to establish a model of evolution. However, the investigation and use of three nuclear microsatellites showed them to be highly polymorphic and therefore useful tools to investigate the genetic variation of taro in Africa.

Taking these issues into consideration, the application of other disciplines such as history, archaeology, ethnobotany and linguistics can add some important insights into taro's arrival in Africa, and provide some food for thought to the reader and future researchers who seek to shed more light on this topic.

FIRST HYPOTHESIS

The first hypothesis proposed for the introduction of taro into Africa asserted that it arrived via the Nile. Three main alternative dates have been suggested for this dispersal. Reindhart (1911 in Rivers, 1926) suggested that taro was introduced ca. 500 BC, while Burkill (1935) proposed that it arrived in the Mediterranean area around the first century AD. Watson (1983: 68) did not specify a date but, based on linguistic data, he suggested that Arabic-speaking peoples dispersed taro in the tropical and semi-tropical regions of Africa, and that from the Arabian Peninsula, taro was translocated to the Mediterranean from where it was possibly introduced to West Africa. Watson's hypothesis is in fact a combination of both northern and eastern entry hypotheses, which are potentially significant in regard to the present study. Al-Masudi's reference (1864) to Egyptian *colocasia* and to *keladi* in East Africa suggests that by the 10th century, taro was present in both East Africa and Egypt.

In this respect, it has been shown that although *colocasia* might initially have been a word for the lotus plant, it later became associated with taro from at least the 7th century AD. Indeed, as discussed in the previous chapter, it is likely that already by the 4th century AD, taro was known as *colocasia*. It is accordingly quite likely that the *colocasia* of Egypt known by al-Masudi was indeed taro.

Given patterns of genetic variation observed in the present study for taro in Africa, a northern introduction can be proposed. Limited sampling in the Mediterranean area forces us to treat this conclusion with significant caution, but observations of taro plants growing in Turkey, Greece, Libya and Italy that present a very similar morphology to those identified as the Mediterranean type could indicate that taro is homogenous across the Mediterranean area, representing the remaining source population of an old variety of taro.

In this regard, more specific investigations of Asian and Mediterranean taro populations are required in order to shed light on the provenance of this taro variety and the people who moved it.

SECOND HYPOTHESIS

According to the second hypothesis, taro arrived in East Africa after being transported across the sea by Austronesian-speaking peoples. The limited sampling of taro in Madagascar (due to destruction of collected samples in a major storm that destroyed the warehouse in which they were stored) constrains assessment of this hypothesis. Linguistic evidence does not, however, seem to support an Austronesian introduction, as pointed out by Beaujard (2011). The present research is only able to show which of the clusters of tropical cultivars the Madagascar plants fall into, and this suggests

a recent introduction for these particular specimens. To increase understanding of taro's introduction into this region, further research is required.

THIRD HYPOTHESIS

The third hypothesis was proposed by Jones (1971), who, comparing material culture between West Africa and Indonesia, suggested that Austronesian-speaking people sailed across the Indian Ocean and around the Cape of Good Hope to West Africa where they introduced taro. This study has shown that from the taro samples collected, greater genetic diversity is present in East Africa than West Africa. Furthermore, the current study shows that the distribution patterns of taro varieties in Africa do not support Jones' idea. The hypothesis of an introduction of taro via West Africa is not supported.

Ethnobotanical observations (Dalziel, 1937) have revealed that people in West Africa sometimes claim that taro is an indigenous crop in the region. In addition, the linguistic studies carried out by Williamson (1970) suggested that the diversity of names used for taro indicate it to be an old crop. However, in the present study, it was shown that taro is present in such countries such as Chad and the Central African Republic; these areas might have represented the regions through which taro travelled from North Africa

to the West or from East Africa through the west. In this study, it was not possible to collect samples from the Central African Republic.

CONCLUDING REMARKS

The results of the genetic, historical and ethnobotanical research undertaken in the present study have been outlined and the three hypotheses put forward to explain the introduction of taro to Africa tested, to the greatest extent possible, against the data produced. Figure 79 summarises the work of Ibrar Ahmed at Massey University, New Zealand, combined with the work carried out in this study at the University of Oxford and University of Warwick by the author, in which the resulting picture appears to show that at least two key dispersal routes were involved in the introduction of taro to Africa.

The first route implies an introduction of taro into the Mediterranean area at an as yet unknown point in time. Research into available historical records for the region suggests that this must have happened before the 4th century AD, when taro was already known and grown routinely in the Mediterranean area. According to this study, a type of taro, indicated as the Mediterranean type, is widely present in Cyprus, Italy and Egypt. On-line research shows that similar morphological types of taro are also likely to be growing in Turkey, Greece and Libya. In Africa, the Mediterranean type is

present in Cameroon, Kenya and in the Arusha region in Tanzania. Since the Mediterranean type was not found along the coasts of East Africa, the present distribution suggests that it reached Africa via the Mediterranean basin, following land routes that connected Asia with this region. According to Ahmed, the Mediterranean type belongs to a Southern Asian cluster, but it is not yet possible to identify the place of origin or departure of this plant, leaving trajectories open to speculation due to the absence of information on the distribution of this clone outside Africa.

The second route may have involved a mixed land-sea route where taro arrived in Yemen and East Africa. According to the present study this type of taro is the most frequent variety, characterised by acrid taste and medicinal properties still exploited in some African countries. According to Ahmed this type of taro belongs to a group of cool-adapted triploids of probable Himalayan origin. Historical accounts and presence distribution of this type of taro in Africa suggests that it entered Africa via the Horn, where it could have been cultivated before spreading inland.

So far, the absence of these two types of taro from sampling undertaken in Madagascar makes the involvement of this country problematic at this stage. More generally these results are by no means conclusive, more realistically presenting a first step towards a better understanding of taro's arrival and subsequent spread in Africa. This preliminary, multidisciplinary study has provided some intriguing insights,

but also raised further questions for future researchers. The involvement of on-the-ground collecting of plant samples and ethnographic data, laboratory research and investigation of textual sources represents a unique interdisciplinary approach that presents both challenges and opportunities.

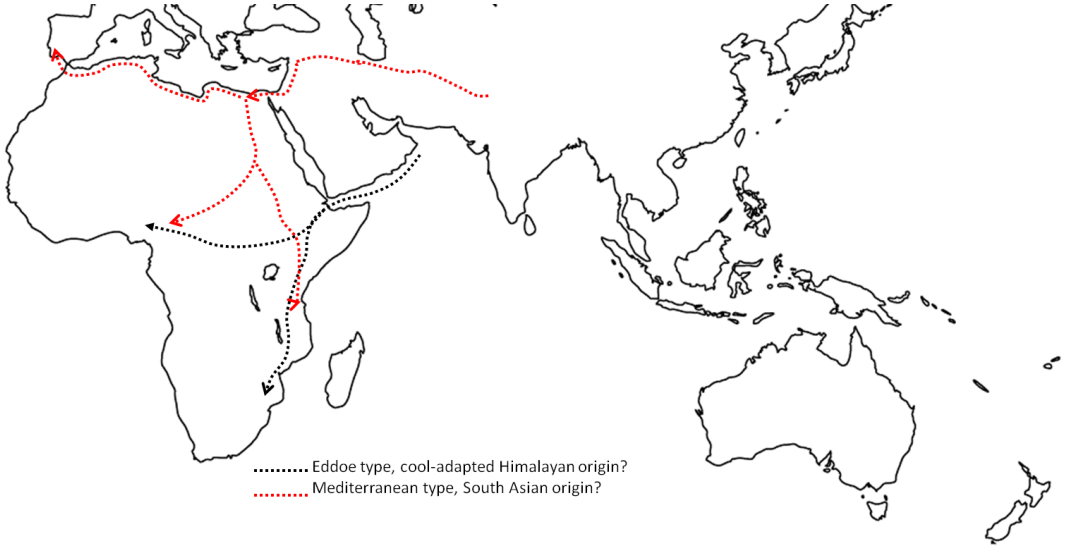


Figure 79. Correlation between Ahmed's results and the present work. The map indicates two independent routes of introduction of taro into Africa. The points of origin are not defined.

CHAPTER 8 CONCLUSION

In this dissertation, the genetic analysis conducted on taro (*Colocasia esculenta* (L.) Schott) has been reported. The evidence has been reviewed alongside other research work on taro including ethnobotanical observations and ethnographic studies across Africa and beyond, as well as contemporary and historical sources from the literature.

This work is the first broad scale study on the genetic variation of taro in Africa, with this plant being used as a partial proxy to trace past human movements, trade and exchange. Plant material was collected in Africa, as well as selected samples from Asia and the Pacific region, which were used to assess and compare the geographical composition of African taro populations. I will now conclude by restating the original aims outlined at the beginning of this research, then I will consider the objectives achieved, after which I will return to the research questions originally set. Finally, a discussion of any limitations will be outlined and a review of opportunities for future work will conclude this thesis.

AIMS

The primary aim of this research was to use taro genetic information to shed light on early human activities in the Indian Ocean, as well as helping to

improve knowledge of its history in Africa. In this regard, it is now possible to state that a significant contribution has been made to the body of genetic data and history of taro in Africa, and that this plant has great potential to illuminate human activities and connections between Asia and Africa in antiquity.

OBJECTIVES

The first objective that was set out in this research was the analysis of the genetic pattern of taro in Africa. In this regard, one of the more significant findings to emerge from this study is that there are at least two main types of taro in Africa; however, within this main sub-division another four varieties of taro can be detected. The four main varieties of taro correspond to tropical and subtropical cultivars originally of Asian extraction, which are cultivated in the temperate and tropical regions across Asia and the Pacific. In chapter 5 on the genetic results, the present work has been combined with that carried out by Ibrar Ahmed in New Zealand on the chloroplast genome of taro. From this combination, it is strongly suggested that taro in Africa is not represented by one single genetic type of plant, and this has to be taken into account when considering how crops were used in the more complex picture of human dispersion.

The second objective was the genetic investigation of the taro corm retrieved at Quseir al-Qadim, in Egypt. In this regard, the archaeological retrieval has been important in providing an absolute date for the presence of taro in Africa, and in this study it was possible to assign the sample to one of the two main chloroplast groups. Unfortunately, it was not possible to find a relationship between this sample and modern taro, meaning that its original Asian provenance has not been resolved. Recently, new molecular markers have been characterised, and their use together with the application of more suitable techniques, would certainly improve its genetic characterisation and ultimately offer important insights into its point of origin.

The third objective focused on improving the ethnobotanical knowledge of taro in Africa. In this context, a three month period of fieldwork conducted in selected countries has helped to achieve a better understanding of taro. One important aspect, which was confirmed from ethnographic research during this study, is that although taro is a crop that is used mainly for its edible starchy corms, it is also evident that in Africa there is a particular taro that is believed to have curative properties by people to a significant degree. Indeed, the use of taro as a medicinal plant to cure stomach problems is also attested to in the historical literature, and it might have been of paramount importance during earlier times when cures for diseases were dealt with solely by using natural resources. To date, medicinal properties of taro have not been systematically researched, and the use of "wrong" varieties (i.e varieties of

taro with little or no medicinal properties) may have led to erroneous conclusions. Any further studies would need to take this issue into account.

The fourth objective focused on the historical research of taro. During this study, new written texts have been uncovered which have enabled greater insight into the history of the plant. Similarly, research into other linguistic and geographical areas may bring to light new evidence and contribute to a better understanding of people's movement and culture. This seems particularly important in areas like Eurasia, which has acted as a bridge between the European and Asian continent. Likewise, understanding of linguistic gaps in Africa might shed more light on internal trade and migrations, perhaps helping to resolve such questions as how Madagascar fits into taro translocation in Africa.

RESEARCH QUESTIONS

At the beginning of this study five research questions were set. Each of these will be addressed, together with any new questions that may have arisen. The first research question explored the potential of the genetic features of taro to understand its history of translocation in and outside Africa. In this regard, significant advances have been made towards the characterisation of the genetic structure of taro in the equatorial regions of Africa, with some limited coverage in other regions, such as North Africa, the

Mediterranean area, Ethiopia, and Madagascar. Much can be learnt from this preliminary work, especially when associated with ethnobotanical research. Such work has shown that not all the varieties of taro are currently cultivated, with some being regularly farmed, and others left for times of famine. While a genetic approach can help to distinguish between different types of taro, agronomic characteristics sought by farmers provide hints on the environmental requirements and likely areas of origin for these types of taro outside of Africa. This is evident from the analysis of the eddoe variety, a type of taro with an acrid and strong taste, which is generally cultivated in drier areas. According to the work carried out by the New Zealand team, this type of taro seems to have Himalayan origins, and in Africa is mainly used as a medicinal plant, rather than as food. While current research has not systematically looked into a characterization of medicinal properties of taro, its wide success in Africa raises questions on when and why it was translocated, and consequently chosen ahead of other varieties. Was it the agronomic characteristics or the medicinal properties that were selected by the first individuals who translocated taro? Or should we look elsewhere for the reasons for its selection?

The second research question that was set at the beginning of this research considered the potential of linguistics in learning more about the history of taro in Africa. In Africa, as in other regions of the world, taro is known by many names. During this study, names applied to this plant have

been collected, both from the literature and during fieldwork. Some names have meanings that describe the qualities of taro plants; some distinguish between cultivars that are good for cultivation, and others that are acrid or that have to be cooked for a long time. However, the most striking element is that farmers and people in general know taro only by their local names, and tend to ignore names used in other countries. This is particularly true in bordering countries which share some linguistic background, like Kenya and Tanzania, where people know taro by different names which would suggest that plant material exchange is limited across Africa. However, genetic analysis showed that there has been considerable gene flow within Africa, which is still ongoing, and while strong linguistic and cultural identities are likely to hamper the acquisition of other names outside their own language, a long time span has more obviously contributed to this linguistic discontinuity.

The third research question focused on the uses and processing methods of taro in Africa, and how these could be related to culinary trends. In chapter 4 emphasis was put on differences in taro processing between West and East African countries, and where possible, local dishes were described. In a wide geographical area such as the African continent, differences are by definition evident. These can be related to environmental characteristics, availability of other food material, taste, and more generally to cultural traditions. Overall, it would seem that taro is still considered a minor crop, and where possible, other crops are preferred as food and chosen for cultivation. Nonetheless, in

all countries visited taro plants are always kept in case of necessity, even if just at the margin of fields, highlighting the continuation of a primitive role that taro still occupies in African societies.

The fourth research question was addressed to identify the most likely points and routes of dispersal of taro into Africa. A major finding of the present work was that four main varieties of taro were identified, and that these were probably introduced into Africa through diverse dispersal routes and at different times. In more specific terms, two older translocations can be detected. One of the older introductions seems to have occurred through a land route dispersal from Asia to the eastern Mediterranean. We have called this the Mediterranean type, with linguistic and historical background suggesting that it has been around for at least two thousand years. The second introduction, however, seems to lie at the margins of the Indian Ocean, with the possibility of a strong connection between Yemen and the Horn of Africa. This is the eddoe type, a cool-adapted cultivar that is now found all across Africa. Additional information on its place of origin and domestication is needed, but it is clear that this plant has been extremely successful in Africa.

While more recent introductions into the continent generally have dates which are recorded in the literature, it is less straightforward to set dates for the oldest introductions due to a relative lack of information to base them on. In this respect, the results obtained in this research have a parallel with the work carried out on the banana in Africa. The history of its translocation to

Africa has yet to be fully interpreted, but the data from this thesis contributes additional evidence which at the very least supports the assertion that multiple routes from Asia to Africa were in place for plant movement in antiquity. In view of this scenario, it is maybe time to unpack the crop package, or "tropical food kit" as it has been called, and consider each crop within its own history.

In this research, the patterns of distribution of the two oldest varieties suggest that both the Mediterranean region and the Indian Ocean served as translocation routes, in which Africa and Asia were linked through land and maritime routes, supporting the view of a proto-globalised world. This connects with the fifth and last research question, in which the implications for maritime movements were considered.

Historically, the Mediterranean rim has been important in connecting people during the time of emerging state civilizations. In this respect, the presence of the Mediterranean taro group, or simply "colocasia of ancient people", indicates that one of the first translocations of taro may have occurred from South Asia into the Mediterranean rim at a time when land routes were in place and maritime routes were yet to be fully established. Less can be said about the overall role that the Indian Ocean played in taro translocation; it is not clear to what extent the Indian Ocean was significant in the early human activities linked to taro. This particular issue will necessarily

need to be investigated once the wider history of taro has been expanded and the role of Madagascar explained.

LIMITATIONS

The most significant limitation of this framework rests on the absence, or limited amount of sampling in key areas such as the eastern side of the Mediterranean and Madagascar. The low number of molecular markers used in the genetic study was also a limiting factor. A higher number of molecular markers may be of help in resolving relationships within the two clusters identified with the analysis of the chloroplast. However, it has to be stressed that while wider investigation of the chloroplast and nuclear genome would certainly improve and resolve closer clusters, the clonal nature of taro has been instrumental in identifying the four main groups.

Another issue that it proved not possible to address in this study were the points of departure for taro. In order to answer this question, much wider sampling would be required, especially in likely domestication areas and important trading zones.

FUTURE WORK

The collaboration between the University of Oxford, Massey University, the Japanese National Museum of Ethnology and the University of Warwick

has proved to be extremely significant not only in the exchange of plant material, but also in sharing knowledge, expertise and comparison of results.

What is now needed is an international study of African taro with the involvement of African teams, with Asian teams likewise working with Asian taro - a muticultural synergy of this kind helping to unravel the history of the plant and the human activities associated with it. More specifically, research now needs to focus on key genetic taro groups and historical areas that may have represented crossing points of diverse human culture in antiquity.

In order to understand the processes of taro dispersal within Africa and to improve understanding of its arrival in regions, future work will need to integrate the expertise of genetics, linguistics, anthropology and archaeology. There is, therefore, a need for multidisciplinary work. To a greater extent, the work carried out on taro has proved that the combination of diverse disciplines such as genetics, history and ethnobotany can contribute to a better understanding of the crop. This approach has been paralleled by another Asian plant found in Africa, the banana, where the synergistic work of archaeologists, linguists, and plant biologists has enabled tremendous advances to be made into the history of its domestication and translocations.

It is the hope of the author that the results that have been presented here can serve as a foundation stone on which to build a more complete story of taro in Africa and hence the people that moved with it.

Appendix 1. Sources from which historical and contemporary records of taro distribution in Africa.

Country	Region/Location	Type of reference	Publication
Algeria	Cap Rosa	Floristic	Battandier, J.A. and Trabut, L. (1885)
		Floristic	Quézel, P., Santa, S., and Schotter, O. (1962)
Angola		Floristic	Durand, T. and Schinz, H. (1895)
	Golungo Alto	Floristic	Rendle, A. B. (1899)
	Cazengo	Floristic	Rendle, A. B. (1899)
	PungoAndongo	Floristic	Rendle, A. B. (1899)
Cameroon		Floristic	Ntepe-Nyame, C. (1988)
Cape Verde	S. Antão, S. Thiago, Orgãos		Chevalier, A. and Chevalier, A. (1935)
		Floristic	Täckholm, V. and Drar, M. (1941)
Central Africa	Béreki		Chevalier, A. (1913)
Chad			The Annotated Ramsar List of Wetlands of International Importance. http://www.ramsar.org/cda/en/ramsar-pubs-notes-anno-chad/main/ramsar/1-30-168%5E16481_4000_0__
Comoros			Bosser, J. (1976)
Congo			Täckholm, V. and Drar, M. (1941)
Cote d'Ivoire			Burkill, (1988)
Egypt			Täckholm, V. and Drar, M. (1941)
Ethiopia		Floristic	Durand, T. and Schinz, H. (1895)
	Malo (Gaytsa, Shaasha, Borodda, Ziita, Falaha, Haste)	Agricultural report	Fujimoto, T. (2009)
Eritrea			Engels, J. M., Hawkes, J. G., and Worede, M. (Eds.). (1991)
Gabon			Wilson, J. E. (1979)
Ghana	Akropong, Akwapim	Agricultural report	Doku, E. V. (1967)
		Floristic	Irvine, F. R. (1930)
Gold Coast		Floristic	Täckholm, V. and Drar, M. (1941)
Guinea		Floristic	Pobéguin, C. H. O. (1906)
Kenya		Floristic	Täckholm, V. and Drar, M. (1941)
	East Africa	Herbarium	Mayo S. J. (1985)
La Réunion		Floristic	Bosser, J. (1976)
Lesotho		Ethnographic	Henderson, L. (2007)
Liberia		Agricultural report	Francis, C. A., Davidson, D. J., Massaquoi, R. C., Mulbah, C. K., Massaquoi, W. K., and Beebe, J. (1995)
Libya		Floristic	Hammer, K., Lehmann, C. O., and L'errino, P. (1988)
Madagascar		Floristic	Täckholm, V. and Drar, M. (1941)
		Floristic	Koechlin, J., Guillaumet, J. L., and Morat, P. (1974)
		Floristic	Bogner, J. (1975)
		Floristic	Bosser, J. (1976)
Mauritius		Floristic	Durand, T. and Schinz, H. (1895)
		Floristic	Täckholm, V. and Drar, M. (1941)
		Floristic	Bosser, J. (1976)

Country	Region/Location	Type of reference	Publication
Mozambique		Agricultural report	Oliveira and Fidalgo de Carvalho, (1975)
Niger		Floristic	Vogel, T., Webb, P. B., Hooker, J. D., and Bentham, G. (1849)
Bas-Niger		Floristic	Durand, T. and Schinz, H. (1895)
Nigeria		Agricultural report	Holland, J. H. (1922)
			Täckholm, V. and Drar, M. (1941)
La Réunion			Täckholm, V. and Drar, M. (1941)
Rodrigues			Bosser, J. (1976)
		Floristic	Durand, T. and Schinz, H. (1895)
Senegal	BasseCasamance	Floristic	Berhaut, J. (1988)
Seychelles		Floristic	Durand, T. and Schinz, H. (1895)
Sierra Leone		Floristic	Durand, T. and Schinz, H. (1895)
			Täckholm, V. and Drar, M. (1941)
South Africa	Mpumalanga		Marloth, R. (1915)
	Eastern Cape		Mengistu, M. G., Everson, C. S. and Clulow, A. D. (2012)
	Limpopo Province		Mengistu, Everson, and Clulow, (2012)
	Western Cape	Brochure	http://www.daff.gov.za/docs/Brochures/Amadumbe_1.pdf
	Gauteng		van Rensburg, Shanahan, and Greyling (2011)
Sudan	Kordofan	Floristic	Durand, T. and Schinz, H. (1895)
	Kordofan	Floristic	Broun, A.F. and Massey, R. E. (1929)
	Bahr El Ghazal	Floristic	Broun, A.F. and Massey, R. E. (1929)
		Floristic	Andrews, F. W. (1956)
	Southern and Central	Floristic	Andrews, F. W. (1956)
	Bahr el Ghazal		Täckholm, V. and Drar, M. (1941) Anglo-Egyptian Sudan
Sudan/Uganda		Floristic	Friis, I. and Vollesen, K. (1998)
Swaziland			Antonsson-Ogle B (1984)
Tanganyika			Täckholm, V. and Drar, M. (1941)
Tanzania			Täckholm, V. and Drar, M. (1941)
	Pemba, Zanzibar	Floristic	Williams, R. O. (1949)
	East Africa	Herbarium	Mayo S. J. (1985)
	Pemba	Ethnographic	Walsh, M. (2009)
Uganda	Lake Victoria (known at the time as Ukérévé)	Floristic	Durand, T., and Schinz, H. (1895)
			Täckholm, V., and Drar, M. (1941)
	East Africa	Herbarium	Mayo S. J. (1985)
Zimbabwe			Henderson, L. (2007)
			Murdock, G. P. (1959)

Appendix 2. Itinerary and material collected by the author during fieldwork.

Date	Country	Location	Satellite coordinates	Altitude	Number of samples collected
17-01-2010	DRC	Kinshasa	S 04°20.735′ E 15°19.913′	283 m	10
18-01-2010	DRC	Kinshasa-Kimwenza Université des Jésuites Saint Pierre Canisius	S 04°27.233′ E 15°17.194′	461 m	2
20-01-2010	DRC	Kwango	S 03°26.461′ E 17°18.182′	Not recorded	10
27-01-2010	DRC	Kinshasa	S 04°20.280′ E 15°17.992′	548 m	7
29-01-2010	DRC	Kinshasa	S 04°23.764′ E 15°18.423′	314 m	10
01-02-2010	CAMEROON	Buéa	N 04°15.129′ E 09°22.159′	140 m	20
02-02-2010	CAMEROON	Buéa	N 04°09.369′ E 09°13.844′	975 m	10
03-02-2010	CAMEROON	Buéa	N 04°09.245′ E 09°13.625′	989 m	10
04-02-2010	CAMEROON	Limbe	N 04°00.815′ E 09°12.142	15 m	20
05-02-2010	CAMEROON	Bafang	N 05°09.774′ E 10°03.115′	720 m	26
06-02-2010	CAMEROON	Bafoussam	N 05°31.021′ E 10°21.479′	1276 m	20
07-02-2010	CAMEROON	Bamenda	N 05°59.161′ E 10°08.313′	1219 m	29
08-02-2010	CAMEROON	Bambui (Centre Regional de Bambui, IRAD)	N 06°00.906′ E 10°16.135′	1441 m	30
11-02-2010	CAMEROON	Kumba	N 04°37.201′ E 09°26.856′	614 m	20
11-02-2010	CAMEROON	Mukuya	N 04°18.005′ E 09°25.507′	28 m	15
18-02-2010	KENYA	Kakingo Kiamworia	S 00°59.892′ E 36°48.048′	1948 m	5
18-02-2010	KENYA	Kakingo Kiamworia (down the valley)	S 00°59.942′ E 36°47.957	1893 m	13
24-02-2010	KENYA	Murang'a	S 00°37.625′ E 37°02.869′	1560 m	23
26-02-2010	KENYA	Ena	S 00°29.941′ E 37°34.276′	1321 m	20
03-03-2010	KENYA	Meru (a)	S 00°04.798′ E 37°39.078′	1583 m	23
03-03-2010	KENYA	Meru (b)	S 00°04.798′ E 37°39.078′	1583 m	14
04-03-2010	KENYA	Maua	Not recorded	Not recorded	4
06-03-2010	KENYA	Not recorded (marshlands nearby rice cultivation)	S 00°42.629′ E 37°19.742′	1164 m	10
16-03-2010	TANZANIA	Zanzibar (Bubùbu)	S 06°05.039′ E 39°13.363	17 m	37
17-03-2010	TANZANIA	Zanzibar (Stone Town- School Lumumba)	S 06°09.345′ E 39°12.374′	-8 m	17
18-03-2010	TANZANIA	Zanzibar (Stone Town)	S 06°11.219′ E 39°14.379′	19 m	10

Date	Country	Location	Satellite coordinates	Altitude	Number of samples collected
19-03-2010	TANZANIA	Pemba (Wete)	S 05°03.782′ E 39°44.275′	51 m	10
20-03-2010	TANZANIA	Pemba (Kombe)	S 04°56.655′ E 39°44.842′	24 m	10
25-03-2010	TANZANIA	Arusha	S 03°22.142′ E 36°41.564′	1392 m	28
29-03-2010	TANZANIA	Bunda	S 02°01.844′ E 33°52.357′	1264 m	7
30-03-2010	TANZANIA	Mwanza	S 02°30.913′ E 32°53.877′	1134 m	10
5-08-2010	ITALY	Tropea	N 38°41.000′ E 15°54.000′	61 m	3
26-04-2012	ITALY	Palermo	N 38°07.000′ E 13°22.000′	43 m	none

Appendix 3. Samples collected by third parties.

Collector	Country of origin	Site of collection	Satellite coordinates	Number of samples	Species Information
Dr Peter Matthews	JAPAN	N/A	N/A	1	*Colocasia gigantea* cv ex Nara
Dr Peter Matthews	TAIWAN	Daken	N/A	1	*Colocasia formosana*
Dr Peter Matthews	EGYPT	Kyoto	N/A	1	*C. esculenta* cv ex Cairo
Dr Peter Matthews	JAPAN	Kyoto	N/A	1	*C. esculenta* cv Ishikawa-wase
Dr Peter Matthews	JAPAN	Kyoto	N/A	1	*C. esculenta* cv Dodare
Dr Peter Matthews	JAPAN	Kyoto	N/A	1	*C. esculenta* cv Tono-imo
Dr Peter Matthews	JAPAN	Kyoto	N/A	1	*C. esculenta* cv Kinu-hikari
Dr Peter Matthews	JAPAN	Kyoto	N/A	1	*C. esculenta* cv Kamisho
Dr Peter Matthews	JAPAN	Garden shop Muko City (Kyoto prefecture)	N/A	1	*C. esculenta* cv Kyoto strong
Dr Peter Matthews	JAPAN	Supermarket, Minami-ibaraki, Osaka	N/A	1	*C. esculenta* cv Aka-zuiki
Mrs Gerarda Buffa	DRC	Uvira, Obélisque	N/A	10	*Colocasia esculenta*
Mrs Gerarda Buffa	DRC	Uvira, Harbour	N/A	10	*Colocasia esculenta*
Mrs Gerarda Buffa	DRC	Bukavu Pansi	N/A	10	*Colocasia esculenta*
Mrs Gerarda Buffa	DRC	Bukavu Kanzajo	N/A	10	*Colocasia esculenta*
Dr Steven Goodman	MADAGASCAR		N/A	2	*Colocasia esculenta*
Dr Dorian Fuller/ Dr Nicole Boivin	SRI LANKA	Pattanam	N/A	8	*Colocasia esculenta*
Soeur Saint	DRC	UVIRA	N/A	10	*Colocasia esculenta*
Soeur Saint	DRC	UVIRA	N/A	6	*Colocasia esculenta*
Soeur Saint	DRC	UVIRA	N/A	3	*Colocasia esculenta*
Soeur Saint	DRC	UVIRA	N/A	3	*Colocasia esculenta*
Soeur Saint	UGANDA	Not provided	N/A	7	*Colocasia esculenta*
Dr Dorian Fuller	INDIA	Orissa	N/A	2	*Colocasia esculenta*
Dr Dorian Fuller	INDIA	W. Maharstra	N/A	2	*Colocasia esculenta*
Dr Dorian Fuller	INDIA	Golbai Sasan	N/A	1	*Colocasia esculenta*
Dr Dorian Fuller	INDIA	Rajabasa	N/A	1	*Colocasia esculenta*
Dr Dorian Fuller/Dr Nicole Boivin	SRI LANKA	Kalamatiya	N/A	1	*Colocasia esculenta*
Dr Dorian Fuller/Dr Nicole Boivin	SRI LANKA	Anuradhapura	N 08° 21.441′ E 80° 24.164′	1	*Colocasia esculenta*
Dr Dorian Fuller/Dr Nicole Boivin	SRI LANKA	Mirissa	N 05° 57.201′ E 80° 27.170′	1	*Colocasia esculenta*
Dr Dorian Fuller/Dr Nicole Boivin	SRI LANKA	Thihariya	N/A	1	*Colocasia esculenta*
Dr Paolo Monti	BURUNDI	Rumonge	N/A	6	*Colocasia esculenta*
Dr Paolo Monti	BURUNDI	Bubanza	N/A	10	*Colocasia esculenta*
Dr Paolo Monti	BURUNDI	Minago	N/A	3	*Colocasia esculenta*
Dr Paolo Monti	BURUNDI	Magara	N/A	2	*Colocasia esculenta*
Dr Paolo Monti	BURUNDI	Bujumbura	N/A	2	*Colocasia esculenta*
Dr Dorian Fuller/Dr Nicole Boivin	SRI LANKA	Pattanam	N/A	1	*Colocasia esculenta*
Dr Dorian Fuller/Dr	INDIA	Golbai Sassan, Orissa	N/A	2	*Colocasia esculenta*

Collector	Country of origin	Site of collection	Satellite coordinates	Number of samples	Species Information
Nicole Boivin					
Dr Dorian Fuller/Dr Nicole Boivin	INDIA	Bhubaneswar, Orissa	N/A	1	*Colocasia esculenta*
Mr Jacques Eucaliptus (Sud Savage)	LA RÉUNION	Not provided	N/A	6	*Colocasia esculenta*
Dr Dorian Fuller	ETHIOPIA	Gamo Highlands (Chencha)	N/A	6	*Colocasia esculenta*
Dr Peter Matthews	ETHIOPIA	Not provided	N/A	1	*Colocasia esculenta*
Dr Peter Matthews	OKINAWA	Not provided	N/A	6	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Calabar road, four corner area, Ikom (1)	N/A	1	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Grassfield, Ikom	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Calabar road, four corner area, Ikom (2)	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Lasmoto village	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Efraya village junction	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Efraya village	N/A	1	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Mankono village (Etomi road)	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Otere village (Obudu road)	N/A	1	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Atemaka village	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Forestry Quarters, Ikom (1)	N/A	1	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Forestry Quarters, Ikom (2)	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Okuni-Ikom	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Akam	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Alesi	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Edondon (1)	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Edondon (2)	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Ochon	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Iyamoyong	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Obubra	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Ekori	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Ugep	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Ikot-Anakanoyom	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Uyanga	N/A	1	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Akamkpa	N/A	1	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Odukpani (1)	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Odukpani (2)	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Calabar township (1)	N/A	2	*Colocasia esculenta*
Mr Israel Borokini	NIGERIA	Calabar township (2)	N/A	2	*Colocasia esculenta*
Dr Peter Matthews	AUSTRALIA	N/A	N/A	1	*Remusatia vivipara*
Dr Peter Matthews	N/A	N/A	N/A	1	*C. affinis* var. Jenningsii (Veitch)
Dr Peter Matthews	TAIWAN	Wulu, Taiwan	N/A	1	*Colocasia formosana*
Dr Peter Matthews	ETHIOPIA	N/A	N/A	1	*Colocasia esculenta*
Dr Peter Matthews	PNG	PNG, Kuk Station (Powell Coll.)	N/A	1	*Colocasia esculenta* cv kawaro
Dr Peter Matthews	PNG	PNG, HAES coll., Aiyura, ex Kainantu	N/A	1	*Colocasia esculenta* cv misio'o
Dr Peter Matthews	PNG	PNG, Goldie R., nr P.	N/A	1	*Colocasia esculenta*

Collector	Country of origin	Site of collection	Satellite coordinates	Number of samples	Species Information
		Moresby			cv, budoa
Dr Peter Matthews	PNG	PNG, Mt Orop-Rulna	N/A	1	*Colocasia esculenta* cv dampel
Dr Peter Matthews	PNG	PNG, found at Wunimp	N/A	1	*Colocasia esculenta* cv mit/deng
Dr Peter Matthews	PNG	PNG, found at Wana Wunimp, Rulna	N/A	1	*Colocasia esculenta* cv rom
Dr Peter Matthews	PNG	PNG, Mt Orop	N/A	1	*Colocasia esculenta* cv kimba
Dr Peter Matthews	PNG	PNG, near Wanimp crater	N/A	1	*Colocasia esculenta*
Dr Peter Matthews	HAWAII	N/A	N/A	1	*Colocasia esculenta*
Dr Peter Matthews	PHILIPPINES	Not provided	N/A	1	*Colocasia esculenta*
Dr Peter Matthews	PORTUGUESE TIMOR	Not provided	N/A	1	*Colocasia esculenta*
Dr Peter Matthews	INDIA	Not provided	N/A	1	*Colocasia esculenta*
Prof Dilip K. Medhi	INDIA	ASSAM	N/A	12	
Dr Peter Matthews	EASTER IS	Not provided	N/A	3	*Colocasia esculenta*
Dr Peter Matthews	FRENCH POLYNESIA	Huahine, Society Is	N/A	3	*Colocasia esculenta*
Dr Peter Matthews	PHILIPPINES	Luzon, Ifugao	N/A	7	*Colocasia esculenta*
Dr Peter Matthews	PHILIPPINES	Luzon, Ifugao, Ifugao, Banaue, Bayninan	N/A	1	*Colocasia esculenta*
Dr Peter Matthews	PNG	Ruti	N/A	2	*Colocasia esculenta*
Dr Peter Matthews	PNG	WHP, Ruti, Yeni	N/A	2	*Colocasia esculenta*
Dr Peter Matthews	NEPAL	Kathmandu, from bazar	N/A	2	*Colocasia esculenta*
Dr Peter Matthews	NEPAL	Kathmandu, from bazar	N/A	1	*Colocasia fontanesii*
Dr Peter Matthews	SRI LANKA	Eliya	N/A	1	*Colocasia esculenta*
Dr Peter Matthews	SRI LANKA	Colombo	N/A	1	*Colocasia esculenta*
Dr Marjike Van der Veen	EGYPT	Quseir al- Qadim trench dated 11^{th}-12^{th} sec AD	N/A	2	*Colocasia esculenta*

Appendix 4. Glossary of African words relating to taro used in this report.

Achu	Paste made by boiling and pounding corms of different varieties of *Colocasia* together with local Cameroonian bananas
Bafut	Language of the Niger - Congo languages family spoken in the West Province of Cameroon
Country coco	Term used to indicate a variety of *Colocasia esculenta* that has dark stem colour, small white corms and also grows in dry soil conditions.
Dasheen	Plucknett's definition of a *Colocasia esculenta* variety (C. esculenta var. esculenta), that has a main large corm and may have smaller corms aside
Eddoe	Plucknett's definition of a *Colocasia esculenta* variety (C. esculenta var. antiquorum), that produces a small or medium-sized main corm and aside numerous small edible cormels
Fufu	Typical paste made by pounding corms after boiling until the paste reaches a certain texture
Igbo cocoyam	Term used to indicate a variety of *Colocasia esculenta*. Two types fall into this category; the first one has a greenish stem colour and white corms, the second one can be identified by a red spot located on the upper part of the stalk
Kikongo	Congolese national language spoken in the Bandundu province (DRC)
Kikuyu nduma	Term used in kikuyu lands (Kenya) to indicate a variety of *Colocasia esculenta*
Kimeru	Language spoken around the Mount Kenya (Kenya)
Kiyaka	Congolese dialect used in the Bandudu Province (DRC)
Kokolo	General term used in Lingala (DRC) to indicate a leaf
Kolkas	Arabic term used to indicate the plant *Colocasia esculenta*
Kolokasia	Modern Greek term used to indicate the plant *Colocasia esculenta*
Irio or Mataha	Dish prepared by mixing boiled *Colocasia* (ngirigaca type) leaves together with boiled potatoes, maize, precooked beans and plantains
Langa	General term used in Kiyaka (DRC) to indicate the plant *Lasiomorpha senegalensis* Hay, it is also used to indicate the corms of *Lasiomorpha senegalensis, Colocasia esculenta* and *Xanthosoma* spp. (DRC)
Lingala	Congolese national language spoken in the Kinshasa province (DRC)
Lupenzu	Term used in Kikongo (DRC) to indicate *Xanthosoma* spp
Magimbi or *maghimbi magi*	General term used in Kiswahili (Tanzania) to indicate *Colocasia esculenta* plants
Makabo	Term used in Lingala (DRC) to indicate *Xanthosoma* spp.
Mala	General term used in Lingala (DRC) to indicate a corm
Malamakòkolo	Term used in Lingala (DRC) to indicate *Colocasia esculenta*
Mangua	Term used in Bafut (Cameroon) to indicate the plant *Colocasia esculenta* that has a yellow/off white stem with reddish corms.
Maniangu	General term used in Kiyaka (DRC) to indicate the plant *Colocasia esculenta*
Mantan	Term used in a Bafut dialect (Cameroon) to indicate the plant *Colocasia esculenta*
Matoma	General term used in Kimeru (Kenya) to indicate the plant *Colocasia esculenta*
Musungu crop	General term used in Kiswahili to indicate a crop that was introduced by white people
Muraria riko	Term used in Kimeru (Kenya) to indicate a variety of *Colocasia esculenta* that needs to be cooked overnight in order to be edible

Muthangari mwea	Term used to indicate a variety of *Colocasia esculenta* that has large leaves, it is usually very tall and has a big central corm surrounded by smaller ones
Mwanake	Term used to indicate a variety of *Colocasia esculenta* that has purple stems and small corms. It can produce flowers
Nduma	General term used in Kiswahili (Kenya) to indicate a variety of *Colocasia esculenta*
Nduma ngirigaca	Term used to indicate a variety of *Colocasia esculenta* that has a red spot located on the upper part of the stalk. The rest of the stem is usually greenish
Nyakigoi	Term used to indicate a variety of *Colocasia esculenta* that has a white stem, white corms, is not very tall and is not now used as food
Taro	General term used to indicate the plant *Colocasia esculenta* (DRC)
Tshiluba	Congolese national language spoken in the Kasai province (DRC)

Appendix 5. List of sources from which data distribution on taro in the Mediterranean was extrapolated.

COUNTRY	LOCALITY and/or REGION	YEAR	PUBLICATION
Algeria		1881	Meyer, 1881
	Cap Rosa	1885	Battandier and Trabut, 1885
		1895	Durand and Schinz, 1895
		1941	Täckholm and Drar, 1941
	Stream Bou Redine, between El Kala and Annaba; Stream Oued en Nahal near Cap Rosa; Streams on the Beni Salah mountains	1957	Maire, 1957
		1962	Quézel, Santa and Schotter, 1962
Anatolia		1941	Täckholm and Drar, 1941
Azores		1895	Durand and Schinz, 1895
		1941	Täckholm and Drar, 1941
		1980	Tutin, 1980
Balkan		1941	Täckholm and Drar, 1941
Canaries		1941	Täckholm and Drar, 1941
Cyprus		1977-1985	Meikle, 1977-1985
		1941	Täckholm and Drar, 1941
Egypt		1895	Durand and Schinz, 1895
Eritrea		1941	Täckholm and Drar, 1941
		1991	Engels, Hawkes and Worede, 1991
Egypt/Arabia		1994	Hepper and Friis, 1994
Greece	Rhodes, Crete	1943	Rechinger and Rechinger-Moser, 1943
	Crete	1941	Täckholm and Drar, 1941
	Zante	1901-1904	Haldcsy, 1901—1904
	Crete	1901-1904	Haldcsy, 1901—1904
Italy	Milis (Sardinia); Sicily; Calabria	1854	Bertoloni, 1854
	Rome (Lazio); Naples (Campania)	1857	Parlatore, 1857
	Sicily (river Molinello; San Cosimano)	1905	Cavara, 1905
	Sardinia, Sicily, Calabria	1908	Fiori, 1908
	Sardinia, Sicily	1941	Täckholm and Drar, 1941
	Sicily, Sardinia, Calabria	1982	Pignatti, 1982
	Palermo (Sicily)	2006	Matthews, 2006
	Sardinia, Sicily, Calabria	1923-1925	Fiori, 1923-25
Lebanon	Beirut, Tyre	1933	Post, 1933
Libya		1941	Täckholm and Drar, 1941
		1977	El Gadi, 1977
		1965	Keith, 1965
Malta		1908	Fiori, 1908
	Bahria, Imtahleb, San Martin, Boschetto	1927	Borg, 1927
	Same localities of Borg 1927	1977	Haslam, Sell and Wolseley, 1977
		1982	Pignatti, 1982
		1923-1925	Fiori, 1923-25
Morocco		1941	Täckholm and Drar, 1941

COUNTRY	LOCALITY and/or REGION	YEAR	PUBLICATION
Palestine		1911	Dinsmore, Dalman, and Steurnagel, 1911
	Wadi-Kilt	1933	Post, 1933
		1941	Täckholm and Drar, 1941
Palestine-Jordan		1931	Oppenheimer, 1931
Portugal	Caldas de Monchique	1861-1880	Willkomm, 1861-1880
	Algarve	1913	Coutinho, 1913
	Algarve	1946	Sampaio, 1946
	Madeira	1941	Täckholm and Drar, 1941
	Madeira	1994	Press and Short, 1994
Spain	Malaga Province (Churriana, Alhaurin, Alhaurinejo)	1861	Willkomm, 1861
	Balearic Islands	1921-1923	Knoche, 1921-1923
		1941	Täckholm and Drar, 1941
		1996	Castroviejo, 1996
Syria		1933	Post, 1933
		1941	Täckholm and Drar, 1941
Syria-Palestine-Sinai		1883	Post, 1883
Tunisia		1896	Bonnet and Barratte 1896
Turkey	Içel province (Anamur and Bozyazi)	2001	Şen et al., 2001
		2012	Simsek, and El, 2012
Jordan		1932	Post, 1932
		1933	Post, 1933
Former Yugoslavia (Bosnia and Herzegovina, Croatia, Macedonia, Slovenia, Serbia, Montenegro)		1915	Thonner, 1915
		1980	Tutin, 1980

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