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On the Trail of Taro
An Exploration of Natural and Cultural History

Peter J. Matthews

National Museum of Ethnology

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Preface

In this volume, I introduce an integrated, ethnobotanical approach to understanding the history of a crop that is possibly one of the oldest cultivated food plants known to humankind. Botanical, ecological, genetic, and ethnographic approaches have been combined in order to investigate the history of taro, *Colocasia esculenta* (L.) Schott. It is only through such an integrated approach that certain key questions can be addressed.

On the Trail of Taro reproduces a range of previous work that has been inaccessible and scattered, though foundational for exploring the history of this crop. In Part 1, the first chapter (newly written), introduces the subject, approach, and my own first steps on the trail of taro. It is followed by two short notes (Matthews 1982a, b) published as the fieldwork began in New Zealand. Parts 2 and 3 reproduce my MSc thesis (Matthews 1984) and PhD thesis (Matthews 1990) respectively. Each has been edited for errors, annotated with footnotes, and partly reorganised in order to provide a more readable sequence. All appendices have been combined into one section, all references have been combined into a single bibliography, and a comprehensive index has been added at the end. The compilation thus covers the years 1982–1990, includes herbarium data gathered during a year of study in Germany (1985), and records initial explorations in New Zealand, Australia, and Papua New Guinea. Although some of the laboratory methods reported are now obsolete, the need to integrate natural and social science approaches through fieldwork, laboratory work, archival research, and literature study is still very current, perhaps more so than ever. Basic historical understanding of useful plants may help to reduce dependence on the dangerously small number of crop species that now support the global food system. To conclude the volume (Part 4), I review recent research and consider future directions for the study, uses, and development of taro.

The target audience for this volume includes students and researchers in the agricultural, biological, and social sciences, and anyone concerned with human relationships with plants, the origins of food, and crop development. The trail of taro is what first brought me to Japan in 1990, a country with a rich history of taro cultivation, research, and utilisation. Since 1990, and while employed at the National Museum of Ethnology, Osaka (from 1996), I have conducted further fieldwork in Australia, Cook Islands, Cyprus, Egypt, Greece, Hawaii, Indonesia, Italy, Japan, Myanmar, New Zealand, Papua New Guinea, the Philippines, Taiwan, and Vietnam.

Every garden and every trail is a small monument to human intentions to survive and prosper, to explore and return home. Even as gardens and the trails that lead to them come and go, taro has persisted in pockets of opportunity provided by nature and by human imagination, memory, and neglect. This volume is an invitation to step into the trail of taro, and explore the remarkable history of a plant carried by countless ancestors, in their travels near and far, over thousands of years.

PETER J. MATTHEWS

25TH OCTOBER 2013

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Part 1

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Part 2 (MSc 1984, University of Auckland)

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Part 3 (PhD 1990, Australian National University)

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Present volume

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PART 1

FINDING THE TRAIL

In this part, I explain how I came to be interested in taro as a subject of historical research, linking childhood experiences to later academic development (Chapter One). Two early notes written as part of initial research on taro are reproduced to simultaneously illustrate development of a field work methodology, and introduce the historical subject.

Chapter Two reproduces a note in which I solicited information from readers, while explaining how taro sites could be recorded using the archaeological site record format advocated by the New Zealand Archaeological Association (Matthews 1982a).

Chapter Three reproduces a first report of observations of taro in the Bay of Islands (Matthews 1982b), and raises questions that were addressed by the research described in Part 2.

Chapter One

Introduction (Some Help From the Ancestors)

In living plants we can discover that our ancestors are still with us, insofar as the plants were part of their lives, and remain part of ours. I say this from personal experience, as my grandfather was a farmer and gardener who grew up within a mixed European and Māori community in northern New Zealand. He grew taro in his own garden in Auckland, and passed on knowledge of the plant as a food to my father, who subsequently introduced the plant to me. I never met my grandfather, but could know him through the garden he made, a large garden that completely surrounded my childhood home.

My own interest in plants began with a natural childhood curiosity in the home garden, the many plants and animals living there, and the people who had been there before me. I lived — and came to life — in that garden, spending much of my time caring for birds and other animals, climbing trees, doing garden work, building and using huts. I could always find refuge there in moments of stress. The garden was also our main source of ammunition, in the form of fruits and nuts, for mostly friendly street wars conducted with the children of neighbouring families. When we excavated new space for an apartment under our 1920s house, we found stone tools left behind by the Māori who had cleared forest and gardened there before us¹⁾ (Notes in this volume appear at chapter ends).

As an undergraduate at the University of Auckland, New Zealand, I naturally gravitated to archaeology, botany, and zoology, and especially the more outdoor aspects of these subjects. My studies were led by a more-or-less subconscious wish to see the past, or to travel in time, and more consciously by a wish to explore New Zealand as extensively as I could with limited funds. As a student volunteer on archaeological digs, I enjoyed wonderful opportunities for low-cost travel in time and space.

Ethnobotany was not a subject taught to biology students at my university in the early 1980s, so I learned mainly by doing, with considerable trial and error. The work of previous writers was inspirational. I explored a wide range of literature that in various ways gave insight into natural and cultural history. Perhaps one of the biggest lessons I learned was the importance of open communication with many different kinds of people, inside and outside the university. In my own repeated experience, wide reading and open communication are a powerful combination for discovering unexpected clues and research directions. Serendipity does not happen by chance alone. Through reading, I learned about my research ancestors, who have usually thought ‘my’ thoughts long before me. I discovered the importance of following ideas to their original sources to learn what previous authors actually said, in their own words, in order to understand a subject better.

If anything I have done can be said to be original, it is probably because I have followed existing trails, cross-trails, and faint markings with a definite purpose, but not too much concern about the ultimate destination. Deliberately losing oneself in a forest is perhaps the quickest way to learn what a forest is.

1.1 Writing as a Method

In the academic world generally, there is too much emphasis on writing and publishing as an outcome, after research has been done, rather than as a means of engagement with the work and with other people. Despite the many new opportunities provided by the Internet and electronic media, research writing and publishing remain a bottleneck (Matthews 2004a) in the entire scientific project of the modern world. The following paragraphs and two chapters indicate, among other matters, how writing can be used as a method, for research purposes.

An important impetus for my work on taro, *Colocasia esculenta* (L.) Schott, came from an essay assignment for a course on Pacific Islands prehistory taught at the University of Auckland. The teacher was an American archaeologist who visited the university in 1981 while writing a book on the subject of the course (Terrell 1986). At that time, Terrell was developing ideas about how theories, models, and scenarios of the past are established, reported, and used. In his classes, he repeatedly emphasised the tenuous nature of our understanding of the past, based as it is on extremely fragmentary and often ambiguous evidence. Although my interests in botany and archaeology made archaeobotany an attractive subject, I came to realise that most living plants and animals had been little studied with the goal of learning about the human past, or prehistory. The subject of my course essay was ‘using plants and animals as biological tracers of human migration in the Pacific’, and much of the inspiration for this came from the work of D. E. Yen, including his book, *The Sweet Potato in Oceania* (Yen 1974), and a lesser-known paper entitled ‘Introduction of taro into the Pacific: the indications of chromosome numbers’ (Yen and Wheeler 1968). While reading the 1968 paper on taro, I found that the New Zealand plants examined had not been described, that their present-day distribution and uses had not been reported, and that much more remained to be learned about this crop in my own country and beyond. With encouragement from the Department of Anthropology, I took this subject to the Department of Botany as a proposal for MSc research, and was soon happily making plans to begin a series of journeys by car and boat across the northern half of the North Island and its offshore islands, in warmer regions where Māori agriculture had flourished in the past, and where rural communities of Māori remained strong.

Since time and funds were very limited, I prepared for fieldwork by writing letters to various people around New Zealand, and two short research notes. These were published in the newsletter of the New Zealand Association of Archaeology (NZAA) (Matthews 1982 a, b) in order to solicit information about locations of taro from archaeologists doing fieldwork around New Zealand (see Chapters Two and Three). Archaeologists and anthropologists in New Zealand already were conscious of the

importance of taro as a staple crop in the tropical Pacific, and knew that the plant was cultivated by the Māori long before the 19th and 20th century arrivals of Europeans, Chinese, Pacific Islanders, and other new immigrants. Archaeological site records held by the Association already included records of taro dating back, in one example, to fieldwork conducted by J. Davidson, A. Leahy, and M. Nicolls in 1961 (Mataka Beach, Kerikeri, NZAA Site N11/300, Leahy 1/1/1978). The apparent association between taro and the distribution of archaeological sites was intriguing, and the anthropological research community in Auckland gave me great encouragement in my first steps on the trail of taro.²⁾

Subsequent feedback from correspondents and readers provided me with personal introductions to people in the field, helped decide the survey routes, and generated new information and questions relevant to the subject. This approach, developed for the MSc project in New Zealand, was later employed as preparation for exploration in northern Australia. It approximated the concept of ‘prior informed consent’, which in its broadest sense means explaining to communities and individuals the aims of research being carried out (often literally in this case) in their backyards. I soon found myself being sent from person to person, down the road, across paddocks, and over hills on journeys that led to many wonderful and memorable encounters in remote and unexpected locations. For the first time in my life, I heard the Māori language spoken as a primary means of daily communication, in the rural communities of East Cape and Northland.

Through letter writing I also made contact with D. E. Yen, and was fortunate to receive an invitation to visit the Prehistory Department of the Australian National University (ANU) with a three-month summer scholarship. In Canberra, Yen already had assembled a living taro collection in order to pursue questions raised by the 1968 paper. He also had established good working relationships with the Australian Plant Quarantine Service holding station at Weston Creek, the Australian National Botanical Gardens (where the collection was maintained), the Research School of Biological Sciences (RSBS), ANU (where the laboratory for population genetics specialised in cytological methods), and plant scientists at the Commonwealth Scientific and Industrial Research Organisation (CSIRO) (conveniently located between the university and the gardens). The visit allowed me to learn cytological techniques, observe the chromosomes of New Zealand taro plants carried to Canberra, and thus complete the research needed for the MSc thesis (Matthews 1984; and Part 2 this volume).

1.2 Further Opportunities, and Serendipity

While still in Canberra I was offered an ANU Scholarship for PhD research, and simultaneously an offer from the German Academic Exchange Service (DAAD) for one year of study in Germany. The second offer led me in early 1984 to the University of Saarbrücken and Paul Mueller (a biogeographer who had worked on snakes in the Amazon), and to Barbara Koller at the European Molecular Biology Laboratories (EMBL) in Heidelberg, where I was guided through steps to extract chloroplast DNA from the New Zealand taro plants (which still travelled with me). A bicycle ride and serendipity

eventually took me to the gate of the Max Planck Institute for Molecular Genetics, Dahlem-Zehlendorf, Berlin, an institution previously unknown to me.

In Germany, my primary aim was to gain experience in the analysis of chloroplast DNA as a way to study maternal lineages in taro, and thus track the movement of vegetatively propagated ‘mother plants’ across Asia and the Pacific (see also Chapter Eight, Section 8.3.2, ‘The genetic evaluation of crop plants’). At the Max Planck Institute I met Alap R. Subramanian, a laboratory leader working on the structure and expression of chloroplast genes, and Yasunari Ogihara, a postdoctoral researcher and one of the pioneers of chloroplast genetics in Japan. The basic methods I learned from these researchers were indispensable for the work in Canberra (1985 to 1990), where I completed the PhD research reported here. Despite all the support in Germany (and later in Australia), my attempts to track ‘mother plants’ through chloroplast DNA eventually failed in the test tube. Other efforts were more successful.

An unexpected result of the stay in Germany was having time and sufficient income to visit some of the larger herbarium collections in Europe (Vienna, Paris, Kew, and Oxford), and to use the Berlin herbarium at Dahlem (a stone’s throw from the Max Planck Institute) as a base for receiving specimens from Leningrad (as it was still known) and elsewhere. From the scattered botanical records of taro, *C. esculenta*, and other *Colocasia* species I later developed the first global map of the distribution of taro and its wild relatives (Matthews 1991, and Figure 9.2 this volume), and could begin to speculate on the possible origin and natural range of the species. The technically simple but logistically difficult work of collating botanical records provided a good foundation for later fieldwork in Australia, Papua New Guinea, and other countries since.

1.3 Main Findings

In the winter of 1984–85, while living in Berlin, I managed to write a paper ‘Nga taro o Aotearoa’ based on the work in New Zealand (Matthews 1985). The paper reported the presence of three main introduced varieties of taro in New Zealand, two that are very similar to each other in appearance and uses (var. RR and var. GR) and one that is very different (var. GP). That was a particularly harsh winter, during which the water pipes in some older buildings froze solid. Jumping from winter in Germany, I arrived in the searing dry heat of Canberra, and then promptly jumped again to the humid swelter of Papua New Guinea to begin fieldwork under the guidance of Douglas Yen. Despite culture shock and physiological shock, the support of our counterparts in Lae allowed me get a glimpse of taro flowering and fruiting in apparently natural habitats (Matthews 1987) and to assemble a living collection of local cultivars that were sent to Canberra for further study.

In Australia, further letter writing was carried out to solicit information on wild taro across northern Australia, leading me to target Queensland for extended fieldwork in 1987 (and again in 1992). In Queensland, wild taro was found scattered throughout the wet rainforest zone of northeastern Queensland. Following the work in Australia and Papua New Guinea, I could announce the existence of ‘a possible tropical wild-type taro’

(Matthews 1991), thus providing circumstantial botanical support for previous suggestions that taro might have been domesticated in New Guinea. In subsequent papers I recommended the use of genetics to investigate prehistory using taro and aerial yam as examples (Matthews and Terauchi 1994), explored the use of insect associates (especially taro planthoppers) as possible indicators of natural range and dispersal routes (Matthews 1995), provided ‘a field guide for wild-type taro’ (Matthews 1997; and Appendix 22, this volume), and discussed the question of how to distinguish natural and feral populations of wild taro in relation to the movements of Austronesian speakers in Asia and the Pacific (Matthews 2003). I also analysed the highly polymorphic ribosomal RNA locus in taro, developing DNA tests that were later used to characterise Japanese cultivars held in a collection at the National Institute for Vegetables Ornamental Plants and Tea (NIVOT) (Matthews, Matsushita et al. 1992).

1.4 Research Questions and Present Volume

Here is a basic general question regarding crop history:

- (1) *By looking at modern (living) plants, how can we learn about the natural and cultural history of a crop?*

This can be addressed by considering a range of more specific questions:

- (2) *What is the natural range of the species?*
- (3) *What are the genetic and geographical origins of cultivated forms?*
- (4) *How was the plant domesticated?*

These in turn lead to more specific questions that may be easier to answer:

- (5) *Where are wild breeding populations (if any) distributed?*
- (6) *Which wild populations are natural or indigenous, and which are invasive, naturalised, or transplanted?*
- (7) *Where are wild relatives of the crop distributed?*
- (8) *Which wild relatives are most closely related?*
- (9) *How are wild populations or wild relatives used?*
- (10) *Which uses of the wild plants might be analogous to very early uses, before cultivation and domestication?*
- (11) *How and where can human selection be effective in changing the genetic composition of the plant, thus creating forms genetically adapted to production and use by people (i.e. domesticated forms)?*

Of course, many other questions need to be asked in order to understand the natural and cultural history of a plant. In retrospect, the initial work in New Zealand can be seen as a series of first steps taken in order to gain familiarity with taro, and with methods for gathering, recording, and reporting information. While working in Australia and Papua New Guinea, further basic questions and theoretical issues became obvious, and approaches for answering some of the questions listed above began to emerge.

As the work proceeded, it also became apparent that there had been — in studies of crop plant history — a general lack of empirical observation, theory building, and theory

testing. Yen's work on the sweet potato in Oceania (Yen 1974) was a notable exception, and provided a template for a more theoretical approach that is still relevant today (cf. Fuller 2013). Modern biology, beginning in the early 20th century and now providing a vast array of methods for analysing plant genomes and phenotypic variation, can answer many questions, but this is not enough. There is still a great need for fieldwork, observation of living plants in their ecological and social contexts, and communication with all the people involved in managing, growing, processing, using, and thinking about plants of historical importance. Many students and researchers are based in countries with little money to invest in 'big science'. Big science is typically where crowds gather. There may be better opportunities for original work in less crowded areas. With an ancient, widespread, and little-studied crop such as taro, there is still much important work that can be done with nothing more than a camera, notebook, pen, and a good list of questions.

Until the present industrial era of synthetic medicine, textiles, construction materials, and food, living plants provided the main material foundations for human economic and symbolic life. Most plants that are cultivated now were known and used as wild food sources long before they were cultivated and domesticated, though it is possible that some wild species have only been used in recent times because of food shortages, changes in access to wild plant resources, the extinction of preferred wild species, or changes in food preferences. Knowing which wild species were used in the distant past, and how, is not easy. The difficulty is greatest for soft herbs such as taro, and other root crops, since they have high water content and lack hard parts that can be easily preserved in archaeological contexts (cf. King 1994).

The second part of this volume is a study of the relatively recent history of taro as an introduced crop in New Zealand. This was my first step on a trail into an ever-deeper and wider history of taro as a wild plant and ancient crop in Asia and the Pacific. Future research on taro may lead even further into the natural and cultural history of humankind as archaeological methods develop, as knowledge of the plant accumulates, and as theories regarding human relationships with plants develop (cf. Etkin 1994; Harris 1996a; Ingold 1996; Smith 2001; Mithen 2006; Winterhalder and Kennett 2006). In the present volume, my focus is on initial empirical observation and developing theories of origin, domestication, and dispersal that can be tested by looking in detail at a single crop. Empirical studies of the evolution, ecology, archaeology and ethnobotany of individual crops and their wild relatives are required before we can generalise with any confidence about the origins and spread of agriculture, crop assemblages, and agricultural societies (cf. Harris 1996b, 2006; Blumler 1996).

Deeper understanding of a plant that has been used in many different societies, for thousands of years, may also help to promote respect for the plant as something that cannot and should not be claimed as the property of any single society, state, or commercial entity. This statement applies to the plant, and also to certain kinds of common or shared knowledge relating to the plant, but not to more specific aspects of local knowledge or belief concerning the plant.

There are no clear boundaries between what is common knowledge and what is

local or private knowledge that should not be made public. This can create conflict between obligations to share information, respect the interests of people, and protect biological and cultural diversity (Bannister and Barrett 2004). The present publication conforms to the academic information-sharing obligation. I hope that it also will serve the interests of people — in many different societies — who have long associations with the plant and who care about the plant. The present publication will be useful if it can encourage a general awareness that most cultivated plants in any particular place have a wider social and geographical context. They can represent a living connection between the distant past and immediate present, and also between geographically and culturally distant peoples. Plants are not just inanimate things to be exploited without regard for context or past. To treat them as such devalues plants, the relationships between plants and people, and the relationships among people.

Notes

- 1) For more stories about childhood experiences of wildness, and how these may guide a person's life course, see Nabhan and Trimble (1994).
- 2) Taro sites continue to be recorded by archaeologists, and most records have been from the conservancy regions of Northland, Auckland and Waikato (Furey 2006: 21).

Chapter Two

Notice to Archaeologists Recording Taro Sites¹⁾

Early European explorers (e.g. Cook, Dieffenbach, and Colenso) provide reports of taro (*Colocasia esculenta*) cultivation in Northland, North Island East Coast, Marlborough Sounds, and Taramakau in Westland. It is (not) clear²⁾ that taro persists today in the wild as a remnant from prehistoric cultivation. Although the plant is sometimes recorded by site surveyors, most people are unsure when trying to identify it.

Presently a botanical study of the distribution and variation of taro in New Zealand is being made by Peter Matthews, Department of Botany, University of Auckland. It is hoped that something will be learnt of its use by the Māori. Taro continues to be used in many rural communities, and within historic times there may have been considerable movement of taro about the country. It is important for describing prehistory that all locations where taro is found be recorded so that prehistoric and historic influences can be sorted out. This includes gardens, where owners are amenable.

Records should be made on New Zealand Archaeological Association site record forms and sent to N.Z.A.A. site record file keepers. If possible, send copies directly to the Dept. of Botany — site numbers for the archaeological locations will be added when available.

Taro is often confused with the closely related elephant's ear and sometimes with arum lily when fully open leaves aren't obvious. Leaf blades of all three are shown in Figure 2.1.

If cormels can be collected (only a handful required) during site recording and sent to me this would be useful. Leafless cormels or short stolons may be sent dry in a small cardboard box. I am particularly interested in collections from south of Auckland. Flowering may be observed occasionally in spring and summer but is not known to result in viable seed. Leaves in some areas reach a height of between one and two metres in summer. During winter smaller leaves are produced.

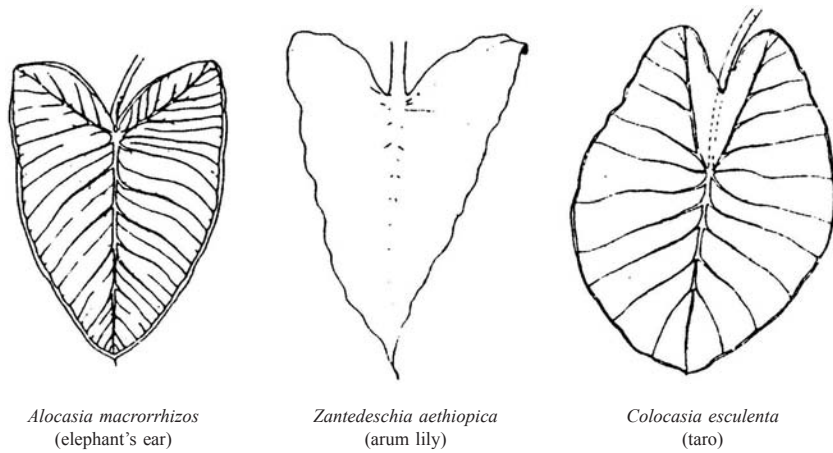


Figure 2.1 Leaf shapes of aroids common in New Zealand³⁾. The *Alocasia* species common as an ornamental or naturalised in New Zealand may be *A. brisbanensis* (L.) Hay.

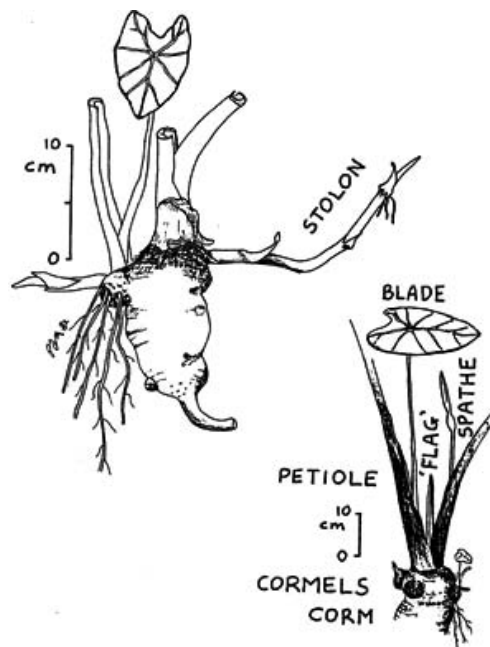


Figure 2.2 *C. esculenta* (taro). Upper: stoloniferous form from Kapowairua (Spirits Bay). Lower: illustrating flag leaf which first appears before flowering (spathe), leaf (petiole and blade), and the easily collected cormels. Scale approximate only.

Notes

- 1) Adapted from Matthews (1982a).
- 2) 'Not' is newly inserted; the original positive statement was made in error.
- 3) Adapted from Healy and Edgar (1980).

Chapter Three

Taro in the Bay of Islands¹⁾

A study is being made of the variation and distribution of taro (*Colocasia esculenta*) in New Zealand. This work has two purposes: botanical exploration, and to provide new information for the discussion of the origins and development of horticulture in New Zealand.

In May 1982 the opportunity was taken to work in the Bay of Islands area with members of the Department of Anthropology, University of Auckland (Sutton 1982) (see Figure 3.1). The aims of the one week of fieldwork were:

To establish what distinct forms are present in the Bay of Islands.

To search for sites with taro, and to determine by casual observation something of the extent of present cultivation as a food crop.

To collect samples for propagation and for counts of $2n$ chromosome numbers.

To attempt application in the field of a scheme for classifying the historical status of taro sites.

This paper records initial observations on the morphology and distribution of two forms of taro found wild in the Bay of Islands. Some problems inherent in the study of New Zealand taro are identified in the light of these observations and historical evidence.

Chromosome numbers have been used to identify likely routes of introduction of taro cultivars into the Pacific (Yen and Wheeler 1968; Cable 1984). Little new information appears to have been published since the 1968 paper. An origin for New Zealand plants in Melanesia was indicated by the discovery in both New Caledonia and New Zealand of plants with chromosome numbers of $2n = 42$. The $2n = 42$ number has not been reported for any other location in Melanesia or Polynesia. On the other hand, taro with the chromosome number $2n = 28$ have been found throughout the South Pacific. The 42-chromosome form has been reported in New Zealand on the Cavalli Islands (Rattenbury 1956), Spirits Bay and Great Barrier Island (Yen and Wheeler 1968). Yen and Wheeler drew no definite conclusion from their discussion of whether this likely introduction from Melanesia occurred before or after the arrival of Europeans.

The present study of New Zealand taro is aimed at establishing whether or not taro of $2n = 42$ can be assigned definite pre-European status in New Zealand. The study must show how varieties are distributed, and whether $2n = 42$ taro exists in such wide distribution or in such remote sites that introduction only after the arrival of Europeans seems unlikely.

Plucknett et al. (1970: 414) and Purseglove (1972: 61) note that the taxonomy of *Colocasia* is confused and that cultivars exhibit considerable variation. Both authors follow Hill (1939) in recognising only one polymorphic species, namely *C. esculenta* (L.)

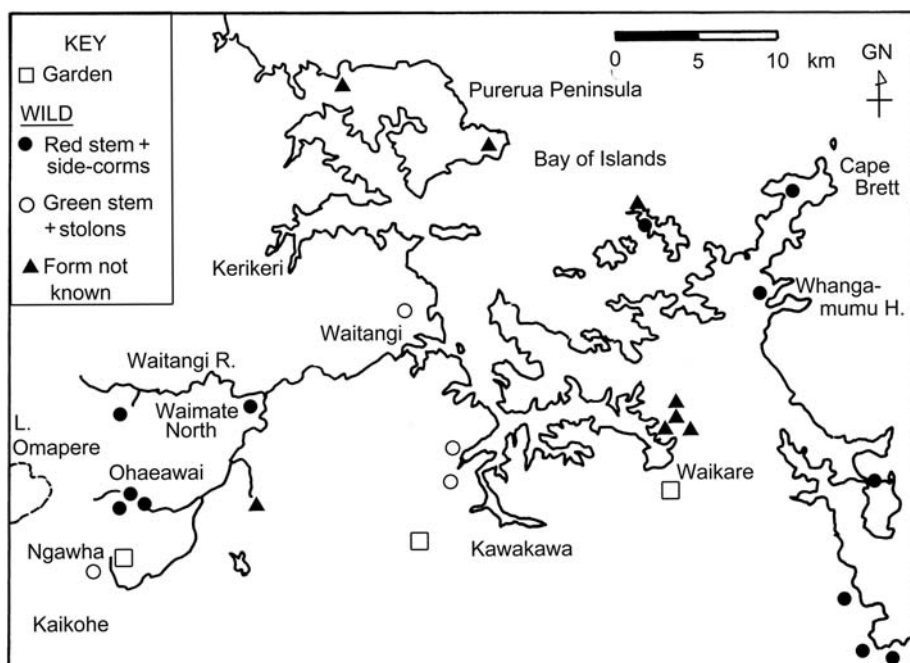


Figure 3.1 Distribution of taro in the Bay of Islands (and vicinity)

Schott. This nomenclature is used by Healy and Edgar (1980) for taro in New Zealand. Plucknett et al. (1970) and Purseglove (1972) do not mention stolon formation by *Colocasia*, but cultivars which produce stolons are briefly discussed by Wilson (1982: 284).

Taro is primarily adapted to moist environments but can grow under a wide range of moisture regimes (Plucknett et al. 1970: 416). The survival of different forms of taro in New Zealand streams or other locations thus provides no indication of how these forms were cultivated. Evidence of pre-European cultivation techniques, wetland or dryland or otherwise, may be found by the study of archaeology, early ethnographic records, and perhaps from present-day cultivators of taro.

Observations of flowering plants by Cooper (1969) and by the present author indicate that viable seed is not produced in New Zealand. Natural dispersal by seed almost certainly never occurs here.

3.1 Field Method

Most sites were located by conversation with farmers and members of Māori communities. To make best use of travelling time, new road routes were taken each day and roadside streams viewed from the elevated position of the rental van passenger seat. Permission was sought before removing plants. Plant samples (cut tops of corms, corms,

cormels, and stolons with nodes) were washed, wrapped damp in newspaper, and stored in unsealed plastic bags in a refrigerator until the return to Auckland.

3.2 Results and Discussion

3.2.1 Variation

Two morphologically distinct forms of taro were found in the Bay of Islands. Both forms have been illustrated by Matthews (1982a) (see Figure 2.2, this volume) using material from outside the Bay of Islands. Although a number of botanical varieties have been described inside New Zealand, it is too soon to assign varietal names to the present forms.

Figure 3.2 shows the acutely lobed, peltate leaves of the form which produces stolons. Cormels were found infrequently on plants of this form. Leaf blades and petioles are a light green. Petioles of up to approximately two metre height were observed.

Figure 3.3 shows the broadly lobed leaves of the form which produces cormels. Stolons have not been observed on plants of this form. Leaf blades are a dark green on the upper surface and light underneath. Petioles have variable red coloration.

A third form is known from the Bay of Islands, but no plants of this form were seen during the May trip. Plants from a garden at Pakaraka (inland Bay of Islands) have been propagated near Whangarei (K. Reynolds, pers. comm.). Figure 3.4 shows the Whangarei plant with a small central corm and many cormels sprouting around it. The petioles of this form are green.

3.2.2 Distribution

The known distribution of taro through inland and coastal areas of the Bay of Islands is shown in Figure 3.1. Host sites on the Purerua Peninsula and in the eastern Bay of Islands have not been seen or visited by the author. They have been located by the reports of residents and visitors and by a computer search of the N.Z.A.A. site records in the New Zealand Historic Places Trust Site Index. The oldest record not since reconfirmed is from about 1953. All the sites shown between Waitangi, Kawakawa, and Kaikohe were either seen or visited during May 1982. All sites are recorded in a botany department site register. Where appropriate, records will be copied for the N.Z.A.A. archaeological site record file. To protect sites, details of location are not published.

The gardens shown in Figure 3.1 are those in which plants are grown as a food crop, with cultivation of the soil. Ornamental gardens are not shown, although two were recorded. Gardens were only viewed from the road, despite their potential ethnographic importance, because present interest centres on wild taro sites. For this reason identifications of morphological form can not be given in Figure 3.1.

Cultivation of taro appears on casual observation to be quite common in the Bay of Islands. Contemporary cultivation in Northland was reported by Ishida (1966: 134) and Yen and Wheeler (1968: 264). On the return to Auckland via southern Hokianga, fifteen food gardens were counted from the main highway. Further south, cultivations were seen at Kaihu near the west coast.

The distribution of wild taro is the product of two factors: transfer and planting by people, and natural dispersal by water. Wild taro sites are those in which propagation is all or almost entirely by natural means, and in which the soil is not cultivated. Many wild taro sites, whatever their origin, are used with varying frequency as food sources. For example, it was learned that taro growing in natural light, boggy ground, behind a marae, is occasionally used during occupation of the marae. Unwanted corm tops and small cormels are replanted at the time of digging. The site has been classed as wild although it lies near the head of a stream, and therefore almost certainly arose by planting at the site.

The above example and many other sites could be placed in a category of semi-wild. However, since information on use cannot be obtained consistently, both fully and semi-wild sites are identified as wild in Figure 3.1.

Wild taro in New Zealand may have had some importance as a food source in pre-European times also, even if taro cultivation was common. Although taro is commonly cultivated, wild taro found in streams and under bush is an important green vegetable for villages throughout Fiji (Thaman 1992: 208–9).

Natural dispersal down streams appears common and was reported by farmers visited during May. One patch was reported washed out in a recent flood of a Waitangi River tributary, with subsequent colonisation of swamp downstream.

A wild taro site at Ngawha (Figure 3.5) was photographed eleven years ago in 1971 by R. C. Cooper, then botanist at the Auckland Institute and Museum. The stoloniferous plants still found there grow in light, boggy ground for a distance of over half a kilometre. In such wet ground the patch could have survived from the scrub or forest burn-off suggested by a surviving stand of large tree ferns.

Taro growing in a swamp in the Waitangi State Forest may have an origin predating the late-1930s clearance of regenerating forest in this area (Mr. Olsen, Forest Ranger, pers. comm.).

Both forms encountered in the wild have widespread distributions within the Bay of Islands. There is an indication that the stoloniferous form may be absent from the eastern Bay of Islands, but fieldwork in the area is needed to establish this point.

The present evidence on distribution suggests that both forms are possibly of pre-European origin. More fieldwork to locate remote sites such as that found in the Waitangi State Forest may provide circumstantial confirmation or otherwise of this suggestion. So too might a search for wider distribution both within and beyond the Bay of Islands.

3.2.3 Collection of propagating material

Samples were collected from ten of the eleven sites visited in the area. Reference numbers for the plants now held in Auckland are AKL 21 to AKL 31. Chromosome counts have not yet been made. A collection of plants is being assembled in Auckland at the Department of Botany and at the Department of Scientific and Industrial Research, Mount Albert.²⁾



Figure 3.2 Acutely lobed, peltate leaves of stoloniferous form (later identified as var. GP)



Figure 3.3 Broadly lobed leaves of form that produces cormels (later identified as var. RR)



Figure 3.4 Whangerei plant (later identified as AKL 34)



Figure 3.5 Taro at Ngawha, May 1982 (a left, later identified as var. GP)

3.2.4 Classification of historical status

Prior to fieldwork a scheme was developed for classifying in a consistent fashion the historical status at taro sites. Categories (definitely old, probably old, probably recent, and definitely recent) were defined on the basis of geographical distance from present settlements and taro cultivations. The basic assumption used was that geographically remote sites have a greater probability of pre-European origin. Such a classification would, in a circumstantial way, aid interpretation of the distributions of different taro varieties. Different varieties might be found consistently in sites of a particular assigned historical status.

The scheme was found impossible to apply for two reasons which became obvious in the field:

(1) The shifting nature of settlement patterns within post-European contact times. Remains of post-contact settlement were frequently met in the field.

(2) The strong likelihood that cultivation and transfer of taro has continued from pre-European times to the present day. Early European records exist of taro cultivation in

the Bay of Islands. Gardens may have been abandoned or provided a source for natural dispersal at any time.

A geographically wide picture of distributions may nevertheless show general pre-European patterns if most movement of plants by people and natural dispersal has taken place within local communities. Diamond (1982) however records the use of taro by Northland's bushmen and other poor rural transients in the first half of the 20th century. These people transferred plants as well as using plants found growing wild.

Further consideration of the above factors affecting taro distribution will be necessary as the study of New Zealand taro proceeds.

3.2.5 Historical records

Wild taro is today distributed on a number of tributaries of the Waitangi River. European records of taro in this catchment span most of the nineteenth century (Nicholas 1817, 1; Cheeseman in Cooper 1969).

In January 1815 (Leach 1980: 136) Nicholas, in the company of Samuel Marsden, crossed the Waitangi River after staying at a village on its banks (Nicholas 1817, 1: 232). Four miles further he encountered thirty to forty acres of kumara and potato plantations at the edge of forest. After passing half a mile through forest he came to Waimate, a fortified village at the summit of a lofty hill. He writes:

'In the plantations adjoining this village, I observed a plant very common in our West India settlements, where it is called *tacca*, and named by the natives of this island *tarro*. It does not appear to me that this plant is indigenous to New Zealand, but must, in my opinion, have been brought hither, either by Captain Cook or some other European navigator who has visited the country.' (Nicholas 1817, 1: 351)

Nicholas also describes the cultivation method at Waimate; plants were in rows 18 inches apart, with the earth dug up and pressed around the roots of each plant. Cheeseman, in February 1895, collected a taro flower at Waimate. The specimen is lodged at the herbarium of the Auckland Institute and Museum and has been described by Cooper (1969).

A number of records exist of the nineteenth century cultivation of European crops in the vicinity of the Waimate Mission Station (Leach 1980). These records were made at different times by the various European visitors to the Mission Station. Wade (1842: 18) describes for January 1838 wheat being gathered in at Rangaunu, close to the Mission Station. He notes that the missionaries introduced European crops amongst the Māori, and that throughout the island the Māori have potato cultivations and in many parts, kumara, taro, maize, pumpkins and gourd. He also states (Wade 1842: 20) that taro is rarely planted to any extent because it fails to multiply at the root like potato. Wade presumably refers to the extent of planting *within cultivations*.

Three points may be made with regard to the above records:

(1) Identifying the origin of New Zealand taro was a problem for Europeans from the time they first observed the plant here. The opinion expressed by Nicholas in 1817 probably reflects ignorance of the Pacific-wide distribution of taro and the voyaging capabilities of Oceanic peoples. Accepting that taro was introduced to New Zealand in

pre-European times does not however deny the suggestion that it was introduced by Europeans from other European colonies.

(2) Taro was displaced in importance by European crops by the early nineteenth century, but nevertheless remained in wide distribution in Māori cultivations. Hargreaves (1959: 62, 64) notes that by the time the first European settlers arrived in the North Island, Māori agriculture had developed to such an extent that it was able to provide the settlers with regular supplies of pigs, potatoes, maize, and wheat.

(3) It is possible to speculate that Wade had observed roots of the stoloniferous taro (Figure 3.2). This is the only form known to the present author that does not multiply at the root by forming (potato-like) cormels that would make extensive planting easy. There is thus a hint that the stoloniferous form presently growing in the Waitangi River catchment was also observed there last century. It is not known with which vegetative form the 1895 flower is associated.³⁾

3.3 Conclusions

The present field evidence together with historical record strongly suggest that taro found today in the Bay of Islands is the same stock as that grown in Māori cultivations early last century.

Taro has probably persisted since that time for two main reasons:

(1) The plant readily grows in the wild and self-propagates vegetatively.

(2) The plant has probably never fully ceased to be used and cultivated as a food crop. Further, by either or both of these mechanisms taro has undoubtedly persisted in the Bay of Islands and elsewhere since pre-European times. Taro of pre-European origin may also persist today in ornamental gardens.

Archaeological evidence may establish the pre-European antiquity of taro cultivation *practices*, but is unlikely to include remains of the soft, herbaceous taro plant. Evidence for the pre-European antiquity of *particular forms* of taro found wild in New Zealand may come from further study of their distribution. For very recent introductions, in the present century, direct evidence may come from importers and cultivators.

Notes

- 1) Adapted from Matthews (1982b).
- 2) This collection was not maintained after conclusion of the MSc project, but some accessions were taken to Australia for further study (see Part 3).
- 3) The observation might also mean that Wade was witness to cultivation of tropical Polynesian (pre-European) introductions of taro that did not produce many small side corms. This contrasts with cultivars found in the 1980s, which do produce many small, potato-like side corms, and are easy to multiply (see Part 2).

PART 2

***COLOCASIA ESCULENTA* IN NEW ZEALAND
*NGA TARO O AOTEAROA***

Here I report results of the New Zealand study introduced in Part 1. Previous accounts of taro in New Zealand consisted of scattered ethnographic records of use and cultivation by the Māori, mainly in the nineteenth century. In previous reports of chromosome numbers in taro, the possibility was raised that New Zealand taro arrived from Melanesia in pre-European times. This suggestion had radical implications for theories of human voyaging and cultural diffusion in the Pacific before written history, since it was (and remains) generally accepted that Māori ancestral and cultural origins lie somewhere in eastern Polynesia.

The research described here was an attempt to determine the historical status of taro present in New Zealand in the early 1980s. Chapters Four to Eight have been adapted from Matthews (1984).

Chapter Four

New Zealand Historical Context and Present Aims

Colocasia esculenta (L.) Schott (taro) is a crop plant not previously described for New Zealand. An initial study of the variation and distribution of taro has been made which provides a basis for future investigation of the plant both within and outside New Zealand. The present research has been directed towards an understanding of the history of taro in New Zealand.

C. esculenta (L.) Schott (taro) is an ancient crop now grown throughout the tropics and sub-tropics in subsistence economies (Plucknett et al. 1970; Herklotts 1972; Leon 1977). Early ethnographic records and Māori traditions (Best 1976) clearly establish that taro was introduced to *Aotearoa* in pre-European times.

Despite the nineteenth century disintegration of traditional Māori agriculture, taro has retained some economic importance. Diamond (1982) recorded the use of taro by Northland's bushmen and poor rural transients in the first half of this century, and Ishida (1966) described taro as a component of contemporary subsistence gardening in rural Māori communities of the North Island. Cultivations were also briefly noted in these communities by Yen and Wheeler (1968) and Matthews (1982b).

Some cultivation is found in the Chinese community (Yen and Wheeler 1968) but was not investigated in the present study. Casual observation indicates that taro is quite widespread in the urban Auckland district, where it is cultivated as a leaf crop in the gardens of Pacific Islander households (J. Watson, pers. comm. 1982).

A large demand for imported taro corms exists amongst the various Pacific and Asian ethnic groups in New Zealand. Imports from the Pacific Islands amount to approximately 49×10^3 kg per week (J. Watson, pers. comm. 1982).

Chromosome numbers have been used to identify likely routes of introduction of taro into the Pacific (Yen and Wheeler 1968). An origin for New Zealand's taro in Melanesia was indicated by the discovery in both New Caledonia and New Zealand of plants with chromosome numbers of $2n = 42$. Taro with this chromosome number also have been recorded in the Solomon Islands of Melanesia (Jackson et al. 1977), and in Timor, the Philippines, the Rykuyus, Japan, China, and India (Yen and Wheeler 1968). The $2n = 42$ number has not yet been reported elsewhere in the South Pacific east of New Caledonia. On the other hand, taro with a chromosome number of $2n = 28$ have been found throughout the South Pacific and in Asia (Yen and Wheeler 1968). Yen and Wheeler (1968) drew no definite conclusion from their discussion of whether the possible introduction from Melanesia occurred before, or after, the arrival of Europeans in New Zealand. The present research was undertaken in an attempt to resolve this discussion.

In recent years there has been considerable international interest in the conservation

of crop genetic resources (Frankel and Hawkes 1975; Simmonds 1979; New Zealand Nature Conservation Council 1980; Plucknett et al. 1983). Apart from the common potato (*Solanum tuberosum*), little is known about the many important root and tuber crops, including taro. Traditional methods of taxonomy do not appear to work well with root and tuber crop species (Leon 1977). Nevertheless, ethnobotanical studies by botanists and anthropologists have provided important insights into the interactions of cultivators and crop-plant gene pools (for example, Panoff 1972; Yen 1974; Jackson et al. 1980; Sillitoe 1983). Yen (1974) and Jackson et al. (1980) combined observations of cultural practices with botanical observations of morphological and cytological variation, and of distribution, in studies of sweet potato and potato respectively. A similar ethnobotanical approach was taken in the present study of New Zealand taro.

For the present report, observations of natural growth and dispersal of taro were made and, where possible, associated cultural practices were recorded to provide insight into possible historical explanations. These observations were made during wide-ranging field surveys. Botanical descriptions of New Zealand taro are presented in the chapters that follow, based on material observed in the field and in a living plant collection. Informal nomenclature is adopted and the New Zealand taro are described as 'variants'. Observations of root-tip chromosome numbers and karyotypes were made on fully provenanced accessions held in a living plant collection.

Three common variants of taro were found to be widely distributed in the North Island: var. RR (red petiole and rounded blade); var. GR (green petiole and rounded blade); and var. GP (green petiole and pointed blade). The distributions of these variants differ in both geographic range and in relationship to human settlement. Each has a chromosome number of $2n = 42$. Two variants with the chromosome number $2n = 28$ were found but are rare and have little or no economic importance in the areas surveyed.

These observations lend circumstantial support to the suggestion of a pre-European introduction of taro with $2n = 42$ from the western Pacific, but alternative explanations are readily apparent. The observations of natural and artificial dispersal have important implications for future studies of the evolution of taro and its relationship with people.

Chapter Five

Taxonomy and General Observations

5.1 Introduction

In the course of field surveys in the North Island of New Zealand, three variants of taro with major distributions were recognised. Observations of growth habit and flowering, and a key for their identification, are presented here. Their cytology is reported in Chapter Six, and their distributions are described in Chapter Seven.

Six other variants of limited known distribution are noted but not discussed. Use of the botanical name *Colocasia esculenta* (L.) Schott follows Hill (1939) and Purseglove (1972), and refers to a polymorphic species of the tribe Colocasioideae and family Araceae. The term ‘variant’ represents informal nomenclature adopted for the present study of variation in New Zealand taro. Where other authors referenced have used the term ‘variety’ in either a formal or informal sense, that use is retained here.

Taro is the Māori common name for *Colocasia* in New Zealand, and is cognate and synonymous with Polynesian terms such as *kalo* and *talo*. Taro also is presently a common name used generally in the Pacific and in literature, and is applied both collectively and singly to the edible aroids *Alocasia*, *Colocasia*, *Cyrtosperma*, and *Xanthosoma*.

The taxonomy of *Colocasia* is highly confused, a situation which is considered characteristic of ancient, vegetatively propagated food crops such as *Colocasia* (Purseglove 1972; Leon 1977; Plucknett 1983).

Although nine names of botanical varieties are listed by Plucknett (1983) in the most recent review of the taxonomic literature, their use appears to have been limited by the lack of any readily available descriptions for them. Debate has centered on the species or varietal status of the names ‘*esculenta*’ and ‘*antiquorum*’.

Haudricourt (1941), Massal and Barrau (1956), Barrau (1957), and Cooper (1969) propose two major subspecies or varieties of *Colocasia* distinguished on the basis of floral morphology. Cooper (1969) records the flowering of *C. esculenta* (L.) Schott in New Zealand and describes two varieties as follows:

‘var. *esculenta* (formerly *typica*), in which the sterile appendage of the spadix is shorter in length than the male inflorescence. This variety also has been defined as that in which the sterile appendage is short and is freed when the spathe tube opens. var. *antiquorum* (Schott, Hubbard and Rehder), in which the sterile appendage is equal to or greater than the length of the male flowers. This variety also has been defined as that in which the appendage is longer, and remains caught in the terminal part of the spathe when

the tube opens.’

Further observations of flowering in New Zealand are presented here. Plucknett (1983) states that there are two general types of crop plants in the cultivated *Colocasia*, and that in general they can be delineated as follows:

(1) Plants that produce a large edible main corm with few cormels (sometimes called sucker corms); e.g. four or eight or so. Generally this group has twenty-eight chromosomes and can be grown under a wide range of water conditions, from flooded (as in Hawai’i and other parts of the Pacific Islands) to rain-fed upland conditions. This plant is *C. esculenta* var. *esculenta*.

(2) Plants that produce a small or medium-sized main corm that often may be inedible because of acidity and a large number (fifteen or twenty or so, to as many as forty or more) of small edible cormels. Some cormels may possess some degree of dormancy. Generally this group has forty-two chromosomes and is grown as an irrigated crop like many other vegetables or as a rain-fed upland crop. This group of plants probably developed in Japan or China. This plant is *C. esculenta* var. *antiquorum* (sometimes called *C. esculenta* var. *globulifera*).

In addition to varieties which produce cormels (synonyms: sucker corms, side-corms), Whitney et al. (1939) describe two varieties forming rhizomes or stolons. Stolon formation also is discussed by Wilson (1982). Both growth habits have been observed among the New Zealand variants described here.

Leaf shape in *Colocasia* ranges from ovate to sagittate, and is entire with an acuminate apex and rounded basal lobes (Strauss 1983). A major diagnostic feature of *Colocasia* is the presence of peltate leaves in contrast to the leaves of other aroids having marginal petiole insertion (illustrated by Massal and Barrau 1956; Strauss 1983). An exception is the ‘*piko*’ group of Hawai’ian cultivars, with marginal petiole insertion (Whitney et al. 1939).

The three major variants recognised in the present study were distinguished in the field by leaf shape and colour. A key based on these characters is presented (section 5.3.1), together with a quantitative analysis of leaf shape using data from the field. Only one collection has been made in New Zealand of what may be a ‘*piko*’ variant of taro.

Whitney et al. (1939) present a botanical classification of 200 taro varieties collected largely from the Hawai’ian Islands and from as far afield as China and Japan. Among these they recognise 84 distinct varieties after observation of the collections, for from one to three generations, under cultivation at the Pensacola Branch Station, Hawai’i. Accessions thought to be similar were grown side by side for close comparisons.

The authors classify 74 of the varieties in a key based on vegetative characters. Floral characters could not be observed in all varieties, and observations of some varieties were insufficient for classification.

Observations were made on plants grown under ‘normal’ conditions, and close to the

period of maximum top growth between four to eight months after planting. After this stage, leaves decrease markedly in size until the time of full corm maturity. Whitney et al. (1939) also note that stage of growth affects qualitative characters: the colour and markings of petioles and corm flesh, the development of side-corms and rhizomes, and the branching of corms. Extremes of fertility, moisture, and sunlight also affect both quantitative and qualitative characters.

The above outline of the study by Whitney et al. (1939) is presented for two reasons: (1) it sets a precedent for reducing the number of named varieties when varieties already named according to a traditional folk taxonomy are classified by the Linnaean approach. (In the present study only three variants were recognised, although Best, 1976, presents a list of 45 Māori names of taro varieties; see Appendix 9 for further information); and (2) it identifies environmental and developmental factors affecting phenotype and relevant to the following account of variation in New Zealand taro.

5.2 Materials and Methods

5.2.1 Field measurements and analysis

Field notes and photographs were made to record habitats, growth habits, and flowering. The measurement of inflorescence parts followed Cooper (1969) except where upper and lower parts of the spathe were measured separately. Inflorescences chosen for measurement were generally at uniform developmental stage, with the upper spathe yellow.

Leaf measurement and sampling

Leaves measured within a patch of taro were individually identified by shoot number and leaf position (innermost first). Sites, site sample sizes, and annotated site descriptions are presented in Appendix 5. The characters measured are illustrated in Figure 5.1 and an example data sheet is shown in Appendix 6.

In general the selection and measurement of leaves was made by the author, with another person recording. The measurements were made in centimetres to one decimal place, in general, and to the nearest centimetre with difficult measurements of larger dimensions.

Twelve leaves were generally measured per site per variant. This number was chosen after a pilot total-population survey of 62 leaves at site NZMS 259/1 (Little Barrier Island) in August, 1981 (data not presented), and was subjectively considered sufficient to describe a patch without taking too much time. Occasionally, greater multiples of twelve were recorded when time and the number of plants permitted. For the analysis of leaf shape, the measurements from sites were pooled for each variant to give large samples incorporating the variation of each variant over a wide geographical range.

Selection of leaves for measurement within a site was not random. Taro generally form clumps within which individual plants (shoots) vary widely in age and size. The clumps within sites also vary widely in age and size, and the dispersion of clumps, in non-cultivated and wild sites, appears highly dependent on characteristics of local water

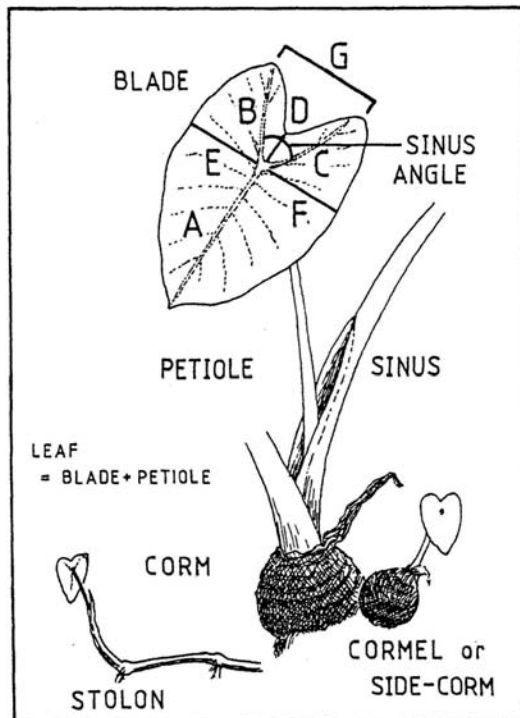


Figure 5.1 Morphology of *C. esculenta*. Illustration of terms and the blade dimensions (A to G) measured to describe shape. (A) to (F) are distances measured from the petiole junction (centre of blade) to edge of blade, and (G) is the distance between the tips of the rear lobes.

flow. In this situation, there is no readily apparent random sampling strategy which can be applied with any consistency from site to site.

In order to minimise the chance of creating apparent differences between variants through sample selection, sampling was aimed at maximising intrasite representation of variation. Leaves were selected which were felt to span the full size range of mature leaves present. Size was subjectively judged largely by the dimensions of petiole height, blade width, or blade length — to what degree shape affected judgement cannot be assessed.

Since leaves at the extremes of size range are less common, most leaves were selected from between extremes, and for this range more or less random walks were taken through patches. No consistency could be achieved with respect to within-plant sampling as the number of measurable intact leaves per plant is determined by its age, the degree to which older leaves have suffered weather damage, and other effects of micro-environment. Some sites contained too few intact, mature leaves to allow much choice about which leaves to select.

Intact, mature leaves were chosen to the exclusion of:

- (1) young leaves not yet fully unrolled and expanded;
- (2) the first, tiny leaves of shooting side-corms, since these have marginal petiole insertion rather than peltate structure — similar to the first leaves of taro seedlings illustrated by Kikuta et al. (1938), and
- (3) ripped, rotted, wilted or obviously malformed leaves.

Analysis of leaf shape

The analysis of leaf data was performed with the University of Auckland central IBM computer using the SAS statistical package (SAS Institute 1982 a, b) and the procedures PROC MEANS (for univariate descriptive statistics) and CANDISC (canonical discriminant analysis).

The statistical theory of discriminant analysis assumes that the discriminating variables have a multivariate normal distribution and that they have equal variance-covariance matrices within each group (in this study, within each taro variant). In practice, the technique is very robust and these assumptions need not be strongly adhered to (Klecka 1975).

Descriptive statistics obtained by the PROC MEANS command indicate that the untransformed leaf measurements are approximately normally distributed with generally slight right-skewness for each of the blade characters measured. Bivariate plots of different combinations of blade characters show scatter increasing with size of character (heteroscedasticity). Log transformation of the data linearised the bivariate plots, and was performed prior to the canonical discriminant analysis to help normalise the multivariate frequency distributions, and homogenise the variance-covariance matrices within each group. Nevertheless, it is suggested that the assumptions required for the discriminant analysis are only approximately satisfied. Because taro leaves are highly symmetrical (Appendix 6), redundant information was present in the original set of characters measured (Figure 5.1). Characters C and F were arbitrarily excluded from the discriminant analysis, and their equivalents, characters B and E, retained with the other blade characters A, D, and G.

5.2.2 Living plant collection

Collection

Accessions to the living plant collection were collected from a wide range of sites during field surveys and also were received from a number of correspondents and other fieldworkers. The accessions were numbered with the prefix AKL (= Auckland) in order of their arrival at the Department of Botany (Appendix 3).

Collection of taro for propagation does not require special care as both corms and side-corms have numerous adaxial meristems in addition to the central meristem. For transport, whole corms, the cut tops of corms (petiole plus top few centimetres of corm), side-corms, and stolon nodal sections were either placed with damp soil in unsealed bags or wrapped without soil in damp newspaper. Under cool or shaded conditions, material was stored for up to two weeks without rotting or dehydration of meristems.

Maintenance

The collection was held in four areas, as space permitted: glasshouse, poly-house, shade-house, and on an outside scoria bed. The plants were generally potted in black PVC bags of sizes PV 3 (100 × 100 × 200mm) and PV 6 ½ (130 × 130 × 280mm). Potting mixes used were fertilised 1 : 1 peat and pumice; and fertilised John Innes soil, peat, and pumice mix (supplied by the Mount Albert Research Centre, Auckland). Plants were multiplied by separation of side-shoots.

Glasshouse plants placed in watering trays were highly prone to spider mite and white fly infestation. Use of insecticide sprays was avoided because leaves were used for a biochemical investigation. Removal of the outermost leaves (usually the most seriously infested) at one- to three-week intervals delayed insect population explosions quite successfully. Periodically all leaves were removed to clear heavy infestations. Plants grown outside and with overhead watering in the poly-house and shade-house remained free of insects.

Observations

Plants were visually checked for constancy in phenotype after removal from the field. Occurrences of flowering were recorded and the inflorescences measured as described above for the field observations. To compare growth habits in variants RR, GR, and GP (described below), cut tops of each were placed in large PV 40 bags (230 × 230 × 460mm) half-filled with brown garden loam, and placed outside on the scoria bed. These were harvested after approximately one year (23.9.82 to 14.10.83) and photographed.

5.3 Observations

5.3.1 A key for distinguishing three New Zealand variants of *Colocasia esculenta* (L.) Schott

An initial key was developed after the first field survey in the central Bay of Islands (Matthews 1982), and with material received from a number of collectors prior to later field surveys. The key below recognises variability observed during the course of these later surveys. Anatomical terms are illustrated in Figure 5.1, and the three variants are shown in colour in Figure 5.2.

- a. Blade peltate, broadly ovate and entire, with obtuse rear lobes. Margins not undulate.
- b. Petioles predominantly greenish bronze to dark carmine, colour development greatest over basal half of petiole (degree of colouration variable within and between plants (younger petioles generally greenish bronze, immature petioles completely green)). Margin of petiole sinus greenish bronze or carmine (variant RR).
- bb. Petioles bright green or yellowish green. Some slight carmine colouring may develop at tip of petiole and along a small distance beneath the blade on the major veins. Carmine colour also appears in a narrow band of variable width along the margin of the petiole sinus (variant GR).
- aa. Blade peltate, ovate and entire, with attenuated rear lobes. Margin coarsely undulate.

Petioles predominantly pale green. Light, greenish bronze colour may develop over more than half the length of the petiole, from base. Some slight carmine colouring may develop at the tip of petiole and along a small distance beneath the blade on the major veins (variant GP).

In practice, variants may be recognised in the field simply as with red petioles and rounded blades (variant RR), green petioles and rounded blades (variant GR) or green petioles and pointed blades (variant GP).

Variants RR and GR are grouped together in the key above because other morphological similarities distinguish them from variant GP (described below).

5.3.2 General observations in the field and the living plant collection:

Areas and dates of fieldwork are set out below:

Northland:

Bay of Islands, May 1982

Cavalli Islands, December 1982

Hokianga to Kaitaia, February 1983

Hauraki Gulf:

Little Barrier Island, August 1981

Waiheke Island, February 1983

Kawau Island, January 1983

Northern Great Barrier Island, January 1983

Coromandel Peninsula, August 1983

East Cape:

Opotiki to Gisborne, January 1983

Habitat range

The limits of habitat range have not been established, since not all areas known to have taro have been explored.

Taro were encountered in a diverse range of habitats, some of which are noted in Appendix 5, or may be seen in Figures 7.1. and 7.2. The most common attribute of sites with wild taro appears to be a plentiful water supply either seasonally, as in small creek or swamp sites, or year-round, as in bigger creek or swamp sites below larger water catchments. The presence of taro in sites lacking natural water flow can generally be attributed to planting by people.

Growth habits (variants RR, GR, and GP)

In the temperate climate of New Zealand the growth of taro is highly seasonal, with a major flush of leaf production over the summer months. Plants in areas prone to frosts, for example parts of Coromandel, were reported by local informants to survive frosts but

with growth set back. Plants with recently rotted and torn leaves were observed in open ground near Waikawau River, Coromandel, during August 1983, and appeared to be damaged by both frost and wind. At other Coromandel sites at this time, plants growing in narrow streams at the entrances of exposed coastal gullies appeared limited in size to the height of the banks which sheltered them.

Conditions that favour large size and a high rate of growth of leaves appear to include shelter, heat, and wet boggy ground (see Figure 7.2).

A clumping growth habit was observed with each of the variants RR, GR, and GP. Clumps in a patch may contain corms and side-shoots varying widely in age. The leaves produced over the summer by young side-shoots attain a smaller maximum size than do leaves from corms a number of years old. Etiolated petioles were frequently observed on shaded plants.

Petioles observed in the field ranged from only a few centimetres to almost two metres in length. Variants could not be distinguished in the field on the basis of size range, although visual comparisons of potted plants indicate that variant GP may be characterised by longer petioles on average than the variants RR and GR.

Variants RR and GR are similar in both their corm morphology and vegetative propagation. They produce undulating central corms with numerous side-corms where the parent is buried or lies against a damp surface. Side-corm production was observed in potted plants (Figure 5.2), and in the field (Figure 5.3).

Corms which have rotted at the base, and dislodged or abscised side-corms, are readily carried downstream by water flow, so that clumps of taro originating from an upstream site may eventually be dispersed within a watershed over considerable distances (to more than one kilometre).

Variant RR has been seen to produce short stolons, but only under highly artificial conditions: in the glasshouse, with roots highly pot-bound, and watered irregularly.

Stolon production is characteristic of variant GP in the field and under all conditions of potting (Figures 5.2 and 5.3). In the field stolons were not always seen, but in all sites prolific side-shoot formation was observed. These appear to grow without an intermediate cormel stage and develop into large corms similar to the parent corm. These side-shoots do not detach as readily as side-corms and it is sometimes difficult to collect propagating material. This close growing habit may be reflected in the extremely dense clumping seen in some sites, covering large areas (possibly more than 1000m² at site N14/30, Reena, North Hokianga).

Formation of stolons appears on casual observation to occur only in dry or damp conditions, rather than in bog or submerged in water. The older corms of variant GP often appear massive compared to those of the other variants (Figure 5.3), but also show undulations. The undulating shape of corms is believed to reflect seasonal growth over a number of years.

Other Variants

Six accessions from Rarotonga, Cook Islands (five of these from a collection at the Totokoitu Research Station, Appendix 3), were maintained in the living plant collection.

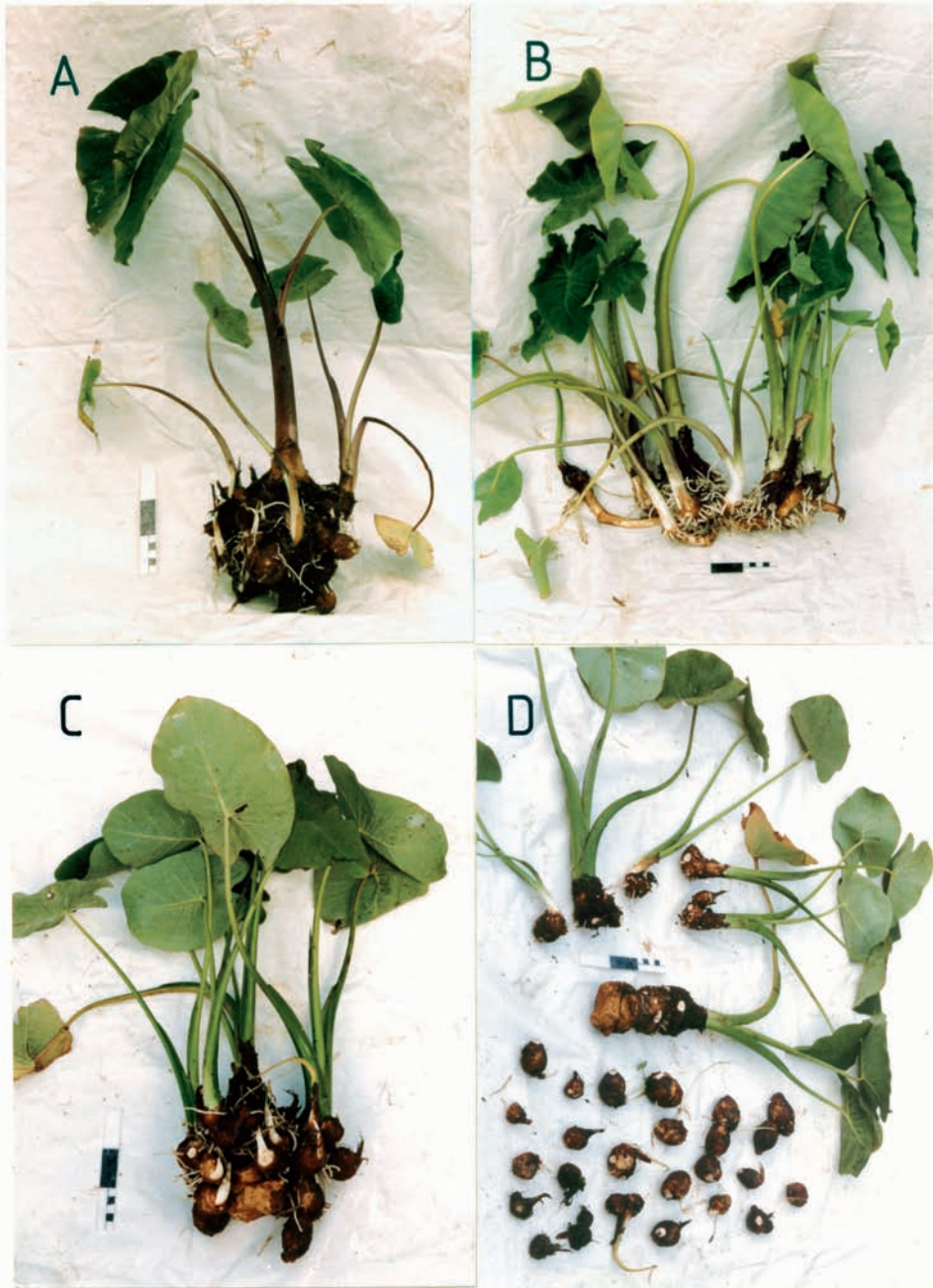


Figure 5.2 Growth habits of New Zealand variants of *C. esculenta*. Plants from potted corms after one year outside (late winter, 1982, to late winter, 1983) at Auckland. Scale bar = 15 cm. (A) Variant RR, AKL 2, tight clump formed with secondary and tertiary side-corms. (B) Variant GP, AKL 29, spreading clump formed with stolons. (C) Variant GR, AKL 37, tight clump formed with secondary and tertiary side-corms. (D) Same as C, dissected.

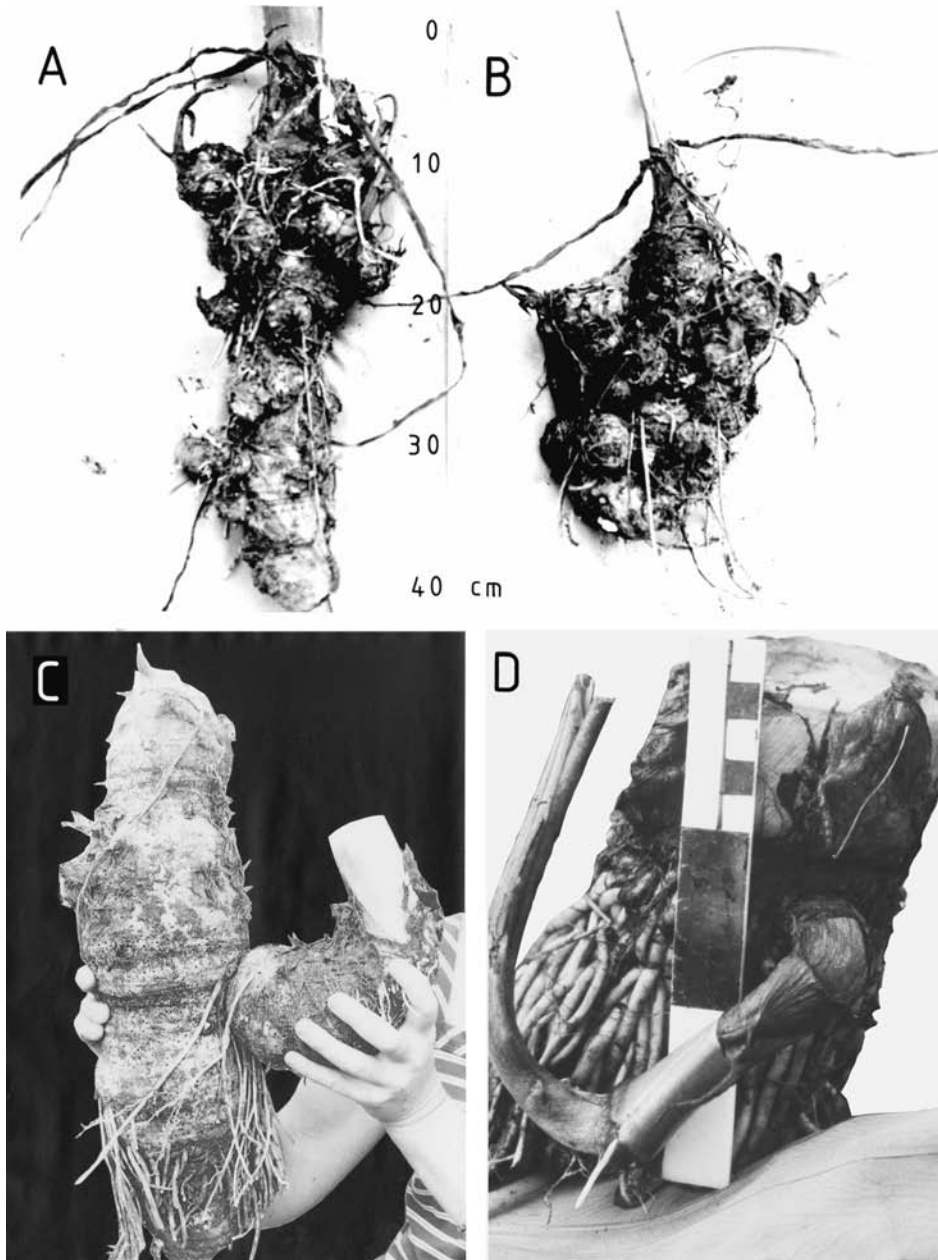


Figure 5.3 Growth habits of New Zealand variants of *C. esculenta*, in the field A and B: from same site (N39/6), Coromandel Peninsula, August 1983; non-cultivated, growing at surface of wet, forest topsoil beside small stream. (A) Variant RR, corm with side-corms; (B) Variant GR, corm with side-corms. C and D: Variant GP, non-cultivated, from boggy ground beside. (C) Corm growing above ground, with secondary corm developed from side-shoot, North Hokianga (site N14/30), February 1983; (D) cut top of corm with petiole base, roots, and stolon. A young root has emerged from the second node of the stolon. The shoot above the second node has had leaves removed. Bay of Islands (site N15/4), May 1982. Scale bar = 15 cm

None of these appeared the same as the New Zealand variants, so descriptions will not be presented.

New Zealand variants collected, other than those already described, are AKL 34, AKL 79, AKL 80, AKL 81, AKL 82, and AKL 87. All of these are known only from single garden sites. Cytological observations have been made on only AKL 34 and AKL 79 (Chapter Six).¹⁾

AKL 34 appears, on limited observation of potted material, to attain a smaller stature than the variants RR, GR, and GP, with shorter petioles and smaller blades. This may be due to its habit of proliferating rapidly, with many tiny side-corms quickly forming shoots around the small, spherical central corm. The size that would be reached after prolonged growth is not known. The blades and petioles are pale green to yellowish green with no traces of red pigmentation. A traced outline of one blade is shown in Figure 5.4.

AKL 79 is like AKL 34 in growth habit but has purple/carmine colouration up part of the petiole, from the base, and in the veins of the blade. The blade has a rather dark appearance. A traced outline of one blade is shown in Figure 5.2.

AKL 80 and 81 are said to differ in petiole length, blade texture, and venation, and whether or not they flower (G. Fuller, pers. comm. 1982, 1983). However, both flowered while maintained in the Auckland collection, and both have very similar general morphology.

AKL 82 is the only variant with marginal petiole insertion and recorded here as '*Colocasia* (?)'. Only one shoot has been observed: the petiole is completely dark purple/carmine, with this colour predominant in the veins of the blade. Staff at Pukekura Park, New Plymouth (G. Fuller, pers. comm. 1983) are familiar with *Xanthosoma* (marginal petiole insertion also) and are certain that AKL 82 is not of this genus. This accession may belong to the '*piko*' group of cultivars noted in the introduction above. A traced outline of one blade is shown in Figure 5.4.

Mutations

At termination, the living plant collection contained fifty-six accessions of variant RR; nine accessions of variant GR; ten accessions of variant GP; and twelve single accessions of other variants or varieties from New Zealand and Rarotonga. No obvious vegetative mutations were observed.

Diseases and pests

All taro seen during the field surveys appeared remarkably free of diseases and pests. Occasionally, leaf damage like that described as 'hopper burn' (Mitchell and Madison 1983) was seen in association with breeding populations of the passionvine hopper, *Scolypopa*.

Four occurrences of possible virus infection were noted in New Zealand taro:

(1) minor vein banding symptoms (feathering) in a succession of leaf blades of AKL 1 (from Little Barrier Island), variant RR, in January 1982, a number of months after collection and growing outside at Mount Albert, Auckland;

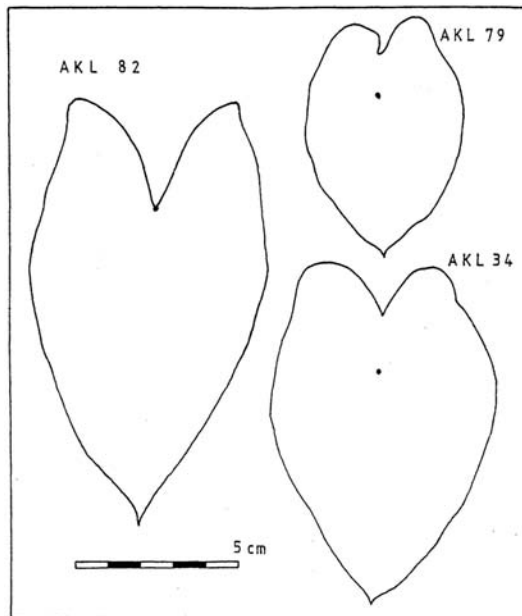


Figure 5.4 Leaf-blade outlines, each from a single leaf. AKL 34 and AKL 79: *C. esculenta*, peltate. AKL 82: *Colocasia?*, marginal petiole insertion. Petiole insertion points shown for each.

(2) recurrent interveinal chlorosis and deformed blade development in a potted plant of AKL 2 (from Little Huia, Auckland), variant RR, in August 1982, several months after collection and growing in a glasshouse in some proximity to virus-infected accessions of taro from Rarotonga (most of the Rarotongan varieties show obvious symptoms of virus infection, Figure 5.7),

(3) yellowed veins over one entire blade (Figure 5.7) in a patch of variant GP, growing wild at Omaio, East Cape (site N70/4), in January 1983; and

(4) chlorosis and deformity (Figure 5.7) in two leaf blades in a patch of variant GP growing wild at Herekino, Northland, (site N9+13/5), in February 1983.

Highly tentative diagnoses of these symptoms are, for each occurrence numbered: (1) dasheen mosaic virus (see Figure 13 in Jackson 1980); (2) dasheen mosaic virus (see Figure 3 in Zettler et al., 1978); (3) small bacilliform virus (see Figure 9 in Jackson 1980); and (4) unknown, symptom unlike previously described symptoms. Re-collection from the original sites, and further diagnostic investigation are needed to confirm these observations as first records of virus infection in New Zealand taro.

In a number of sites the torn ends of petioles indicated browsing by some herbivore. Pigs, goats, horses, sheep, cattle and pukeko were variously mentioned by informants in the field as animals which attack taro. Generally the large stock only eat the tops and

only in times of hunger, while pigs and goats may eat both tops and corms. Pukeko, reported only once, apparently slash the plants while searching amongst them for insects.

5.3.3 Flowering

The inflorescences of *Colocasia* are comprised of a spathe surrounding a spadix that contains zones of female, male, and sterile flowers (Strauss 1983). The structure of an inflorescence and the parts measured are shown in Figure 5.5.

General

Records of taro flowering in New Zealand, both recent and old, are listed in Table 5.1. During summer field work in North Auckland, in February 1983, prolific flowering by variant GP was observed in five sites.

Floral measurements are recorded in Table 5.2. No fruit formation was observed, and older spadices were seen withered and rotted to various degrees at the same time as younger spathes, on the same plant, were seen emerging (Figure 5.6) or shedding pollen.

As it was nearing the end of summer it was thought likely that increasing coolness would prevent any fruit development later.

Table 5.1 Records of *C. esculenta* flowering in New Zealand. For some, site number is given as the origin for collected material, or to specify the location of flowering. Collected material is identified by the plant accession number. Reference numbers for measured flowers are given for cross reference to the measurements in Appendix 8. G = garden; c = cultivated; nc = non-cultivated; d = derelict. For definitions of terms see Chapter Seven.

Variant	Origin	Plant acc. no.	Botany Department site no.	Site description	Flowering location	Region	Date or approx. period	Flowers measured (ref. no.)	Informant
RR	N23/1			G,c	Tekawa Stn	Dargaville	Feb 1983		A. Stilwell pers. comm. 1983
RR	N41/2	AKL 2		Glasshouse potted	Botany Dept	Auckland	Mar 1982	Yes (1)	P. Matthews
RR	?		N41/2	G, nc, nd	Little Huia	Auckland	Oct - Nov		J. Walsh pers. comm. 1982
RR	NZMS259/1	1		Glasshouse potted	Botany Dept	Auckland	Mar 1982	Yes (2)	P. Matthews
RR	NZMS259/1	1		G,c	Mt. Albert	Auckland	July 1982	Yes (3)	P. Matthews
RR	NZMS259/1	1		G,c	Mt. Albert	Auckland	Dec 1982		P. Matthews
RR	NZMS259/1	1		G,c	Mt. Albert	Auckland	Mar 1983	Yes (4)	P. Matthews
RR	N33/1			G,c	Ponsonby	Auckland	May 1982	Yes (5)	I. Lawlor pers. comm. 1982
GR	?		N18+22/2	G, nc, nd	Waimamaku Beach Road	Hokianga	Feb 1983		P. Matthews
GP	?		N14/3	G, nc, d	Mitimiti Rd	Hokianga	Feb 1983	Yes (6)	P. Matthews
GP	?		N14/30	Wild	Reena	Hokianga	Feb 1983	Yes (7)	P. Matthews
GP	?		N9+13/1	Wild	Herekino	Herekino	Feb 1983	Yes (8)	P. Matthews
GP	?		N9+13/10	Wild	Tauroa Pt.	Kaitaia	Feb 1983		P. Matthews
GP	?		N9+13/5	Wild	Ngaire St.	Kaitaia	Feb 1983	Yes (9)	P. Matthews
?	?			?	Waimate	Bay of Islands	Feb 1895		T.F. Cheeseman 1)
?	?			Wild	Lava Point	Raoul Island	June 1956	Yes	R.C. Cooper (1969)
?	Samoa			Garden	Henderson	Auckland	April 1967		T. Harris 1)
?	?			Garden	Henderson	Auckland	March 1964		T. Harris 1)
esculenta	Edmund St			Garden	?	Auckland	Feb 1968		A.T. Pycroft 1)
esculenta	Bay of Islands			Garden	Edmund St	Auckland	April 1962	Yes	A.T. Pycroft 1)
esculenta	?			?	Ngaire Bay	Whangaroa	Dec 1963	Yes	A. Leahy 1)
esculenta	?			?	Kerikeri Beach	Bay of Islands	Dec 1963	Yes	A. Leahy 1)

?	?			?	Mataka Beach	Bay of Islands	Jan 1961		A. Leahy 2)
antiquorum	?			?	?	Kaitaia	April 1921	Yes	R.H. Matthews 1)
antiquorum	?			?	Whareora	Whangarei	Sept 1968	Yes	J.C. Nicholson 1)
?	?			?	Te Araroa	East Cape	'recently'		R. McConnell pers. comm. 1982
?	?			?	?	Northland	Jan		K. Reynolds pers. comm. 1982
?	?			?	?	Northland	May		K. Reynolds pers. comm. 1982
?	?			?	?	Northland	June		K. Reynolds pers. comm. 1982
antiquorum	?			?	Remuera	Auckland	May 1970		Herbarium specimen AK 123004
RR	Opotiki			?	Remuera	Auckland	Feb 1974		Herbarium specimen AK 151544
taroheia	Hokianga			?	Remuera	Auckland	Apr 1980		Herbarium specimen AK 151597
AKL 80	N109/2	AKL 80		Glasshouse, potted	Botany Dept	Auckland	Sept 1983	Yes (10)	P. Matthews
AKL 80	?	AKL 80	N109/2	outdoors	Pukekura Park	New Plymouth	Apr 1983	Yes (11)	P. Matthews, G. Fuller pers. comm. 1983
AKL 81	?	AKL 81	N109/2	outdoors	Pukekura Park	New Plymouth	Apr 1983		P. Matthews, G. Fuller pers. comm. 1983
AKL 81	N109/2	AKL 81 AKL 12		Outside, potted	Botany Dept	Auckland	Dec 1983		P. Matthews
Tonga Sea	DSIR Rarotonga	AKL 12		Glasshouse, potted	Botany Dept	Auckland	Apr 1983	Yes (12)	P. Matthews
Niukini Ava'ava	DSIR Rarotonga	AKL 15		Glasshouse, potted	Botany Dept	Auckland	Apr 1983	Yes (13)	P. Matthews
Malahu	DSIR Rarotonga	AKL 16		Glasshouse, potted	Botany Dept	Auck land	Apr 1983	Yes (14)	P. Matthews

1) See R.C. Cooper (1969). 2) See New Zealand Archaeological Association Site Record Form (NZMS 1) N11/300.

Variant RR, potted in the glasshouse (Figure 5.5) and outside, has been seen to flower and shed pollen. Prolific flowering in patches, as with variant GP, was not observed. Flowers have not been observed for variant GR. This may be partly due to chance: fewer accessions of this variant were collected than of variant RR. Formation of a flag leaf, however, was seen on one occasion in the field. In all instances of the other variants flowering, each inflorescence was preceded by emergence of a flag leaf. Ghani (1982) described the flag leaf as a 'morphological indicator' for flower emergence within the following twelve days. Coarse dissection of variant GR with a flag leaf, however, revealed only young vegetative shoots. Very young or retarded inflorescences may have been missed in this dissection.

Records and measurements of flowering by other taro variants collected are given in Appendix 8.

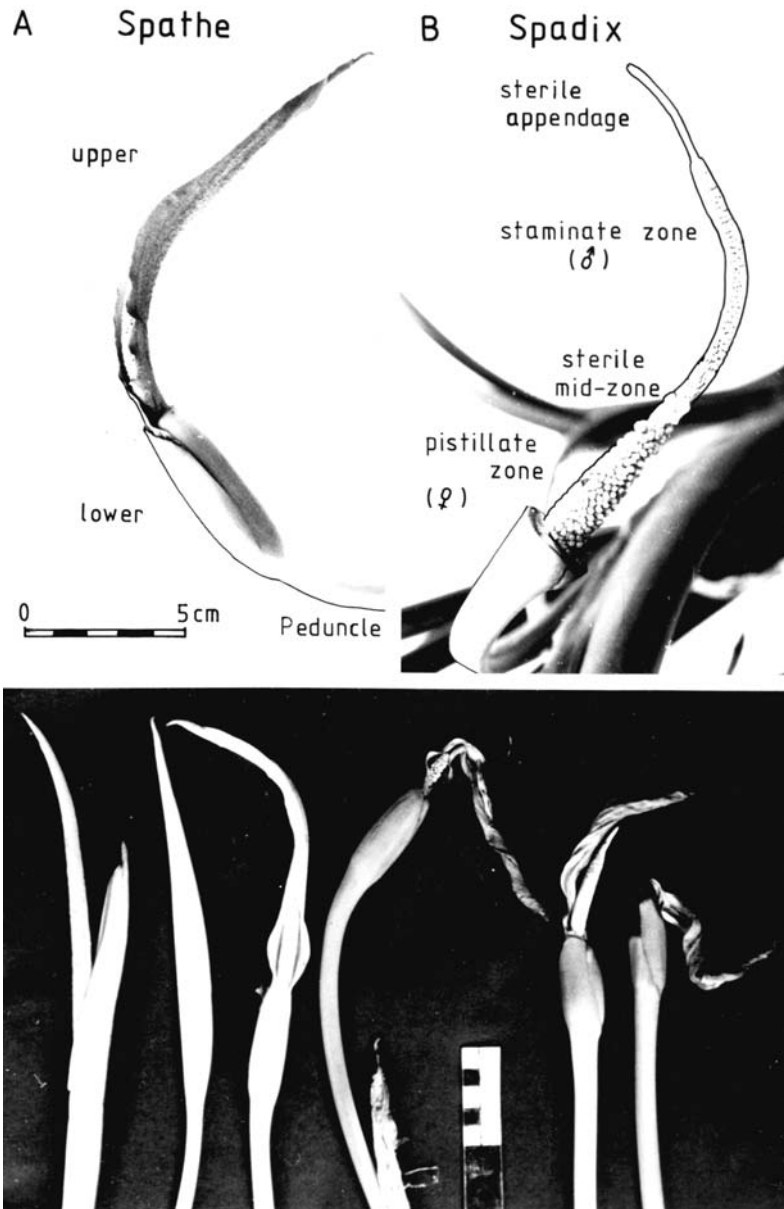


Figure 5.5 Flowering of *C. esculenta* variant RR, in New Zealand. (A) Spathe and peduncle with parts labelled. (B) Spadix with parts labelled. A and B: Accession AKL 2 from Little Huia, Auckland, potted in glasshouse, March 1982. Lower: A full set of four inflorescences from one plant, with the first formed inflorescence at far right. The flag leaves are not shown except for one between the second and third inflorescences, and one before the young leaf (rolled) at far left. The return to vegetative growth is accompanied here by the formation of a pseudo-spathe containing no spadix, and an aberrant flag leaf with a small growth of lamina tissue at its tip (far left). The spadix of the second inflorescence has become free of the spathe, while that of the third inflorescence remains bound within. Accession AKL 1 from Little Barrier Island, Hauraki Gulf, growing outside at Mount Albert, Auckland. March 1983

Table 5.2 Floral morphology of *C. esculenta*. Summary statistics for observations in New Zealand (variants RR and GP, 1982–83; var. *esculenta* and var. *antiquorum* from Cooper 1969) and Hawai'i (field-station varietal collection, Whitney et al. 1939). Data: Appendix 8. Note: Some rounding error is apparent in the calculation of means.

		Spathe (cm)			Spadix (cm)			Staminate Zone	Sterile Appendage	Ratios		
		Total Length	Lower Part	Upper Part	Total Length	Pistillate Zone	Sterile mid-zone			Spathe		Spadix
										Lower/Upper	Sterile Append./Spadix	Sterile Append./Staminate
Variant RR	n	6	6	6	5	5	6	6	6	6	5	6
	X	25.6	5.2	20.5	13.5	3.0	1.8	5.7	3.4	0.24	0.23	0.59
	s.d.	3.5	0.7	2.9	3.6	1.0	0.5	1.1	1.2	0.03	0.06	0.17
Variant GP	n				21	21	21	21	21		21	21
	X				10.9	3.7	1.7	2.9	2.6		0.24	0.96
	s.d.				1.5	0.6	0.7	0.7	0.5		0.03	0.23
var. <i>esculenta</i>	n	6			6	6	3	6	6		6	6
	X	23.6			9.3	3.9	1.9	3.0	1.4		0.14	0.53
	s.d.	3.8			2.5	1.9	0.7	1.7	0.9		0.08	0.43
var. <i>antiquorum</i>	n	2			2	2	2	2	2		2	2
	X	20.3			13.4	3.5	1.7	4.3	3.9		0.29	0.90
	s.d.	3.1			2.2	0.5	0.8	0.8	1.0		0.03	0.06
Hawai'i n=No. of varieties	n	35	34	35	31				31	34	31	
	X	23.3	4.0	19.2	8.3				0.81	0.21	0.10	
	s.d.	5.5	1.0	4.7	2.6				0.31	0.03	0.03	



Figure 5.6 Flowering of *C. esculenta* variant GP, in New Zealand. Left: Whole plant with the first-formed inflorescence (outer-most) withered, and the second at the stage marked by yellow colour of the upper spathe. The spadix of the first inflorescence remains bound within the spathe. Plants in a derelict, non-cultivated garden, northern Hokianga (site N14/3). February 1983. Scale bar with centimetres. Right: Spadix revealed by partial dissection of the spathe. The upper spathe is yellow and pollen is being shed (apparent in roughness at surface of the staminate zone). Gynoecia (green) and stigmas are visible in the pistillate zone.

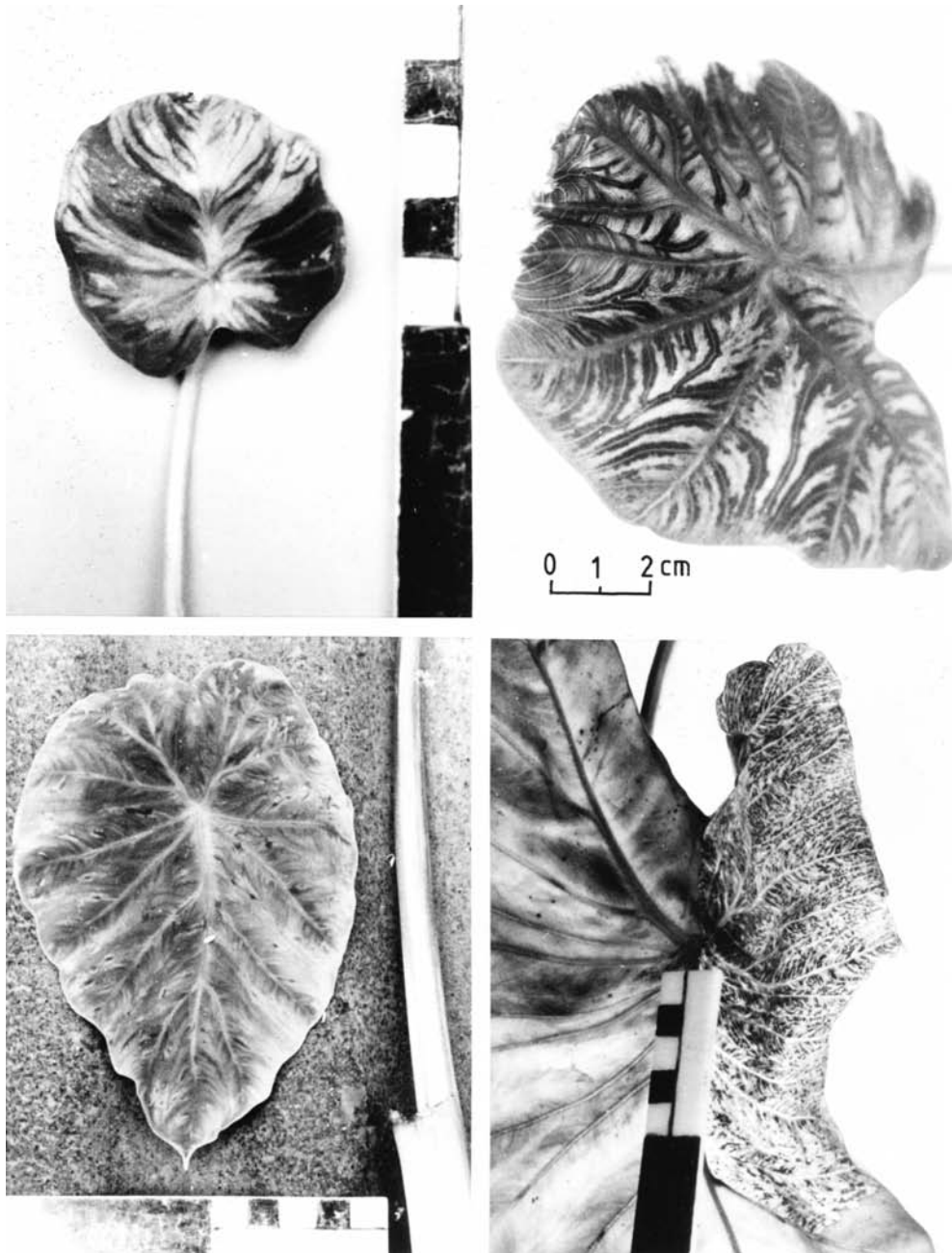


Figure 5.7 Leaf blades of *C. esculenta* with symptoms suggesting virus infection. Upper: Variant RR, AKL 2. Leaves taken at two times during August 1982, from a potted plant in the Department of Botany collection, Auckland. Lower left: Variant GP. Single diseased leaf in a wild patch at Omaio, East Cape (site N70/4), January 1983. Lower right: Variant GP. One of two diseased leaves observed in a wild patch at Herekino, Northland (site N9+13/5), February 1983.

Measurements

A summary of previously published data and the present observations is given in Table 5.2. Generally, the observations are very scanty and incomplete. While Whitney et al. (1939) state that their descriptions are based on turgid material, Cooper (1969) reports observations on dried herbarium specimens and the withered samples brought to him. In withered inflorescences disproportionate shrinkage of the male and sterile parts has been observed (Figure 5.5, lower).

5.3.4 Leaf shape analysis

Leaves of the variants RR, GR, and GP were classified prior to the analysis on the basis of leaf shape and colour, as described in the key above. The observations presented here quantify the characteristics of shape upon which the key is partially based.

Univariate statistics

Descriptive statistics for each of the observed leaf characters and some derived characters are given in Appendix 6.

Means and standard deviations for the blade characters used for canonical discriminant analysis are shown in Table 5.3. These statistics are summarised as the mean blade outlines shown in Figure 5.8. The visually most striking features of the outlines are:

- (1) the attenuation and spread of the rear lobes in variant GP; and
- (2) the similarity between RR and GR.

Multivariate statistics

Canonical discriminant analysis creates axes in the multidimensional space defined by the observed characters. The created axes (canonical variates) provide maximal discrimination between the centroid means of each group (taro variant). In this analysis the number of canonical variates that might provide discrimination is limited to two, one less than the number of taro variants, since the number of observed characters is greater than the number of groups (variants). Two canonical variates are sufficient for discrimination between three groups, assuming that all three are different with respect to characters included in the analysis.

With analysis of \log_{10} transformed blade measurements (Figure 5.9) only canonical variate 1 (CV 1) provides discrimination between the three taro variants. Scores for variant GP are clearly distributed lower on CV 1 than are scores for variants RR and GR, while no discrimination is apparent between the latter.

The largest standardised canonical coefficients (Table 5.3) for CV 1 are found with $\log_{10}B$ and $\log_{10}D$, showing that the characters B and D contribute most to between-group variation along the discriminant function (CV 1).

The reversed signs of these two coefficients show that maximum discrimination is obtained by contrast of large B and small D values with small B and large D values.

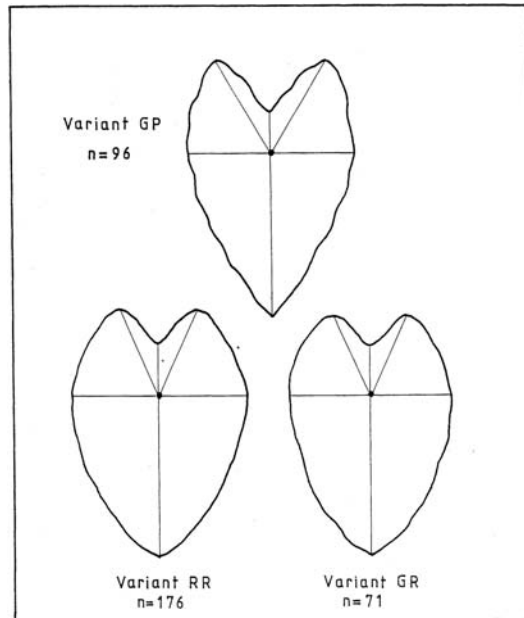


Figure 5.8 Leaf blades of three New Zealand variants of *C. esculenta*. Outlines based on mean values of the linear dimensions shown, depicted relative to the largest dimension of each. The real-size means of the largest dimension range from 20 to 26 cm approximately. Undulation in the margin of variant GP is a characteristic of that variant. The central circle represents the point of petiole insertion.

Close inspection of the blade outlines in Figure 5.8 confirms this interpretation: Variant GP has both longer rear lobes and a shorter sinus-to-petiole distance than variants RR and GR.

Although the spread between rear lobes is noticeably greater for variant GP than the other variants (Figure 5.8), the character (G) proved of minor importance in this analysis. This may reflect relatively low correlation between measurements of characters G and D (Table 5.4) resulting from the relatively high measurement error associated with G. In the field, difficulty was met in measuring G due to the flexibility of the lobes, while other, internal blade dimensions were more easily measured. On the obtuse rear lobes, the absence of a clear point of maximum lobe extension also contributes to error in measurement of G, and also to the derived character, sinus angle.

The blade sinus-angle, $2 \cdot \sin^{-1} \left(\frac{G}{B+C} \right)$, is a further quality which distinguishes variant GP from variants RR and GR, (Figure 5.8, Appendix 6).

However, because it is composed of linear leaf-blade characters related in a non-additive fashion, sinus-angle cannot contribute to the discriminant functions (canonical variates) — the present analysis is based only on the raw measurements of linear characters.

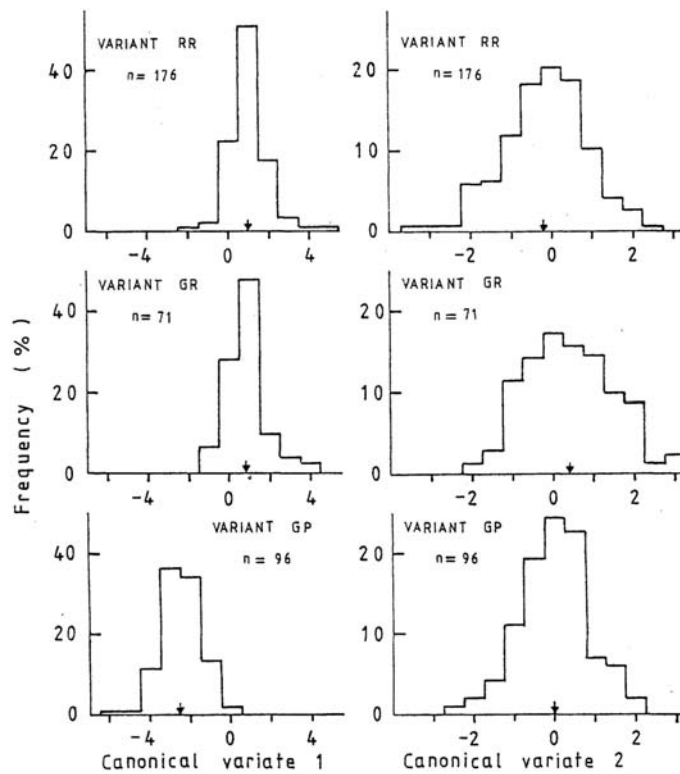


Figure 5.9 Canonical discriminant analysis of leaf shape in *C. esculenta*. Frequency histograms of the canonical scores for the New Zealand variants RR, GR, and GP. Arrows indicate mean scores.

Table 5.3 Canonical discriminant analysis of leaf shape in *C. esculenta*, New Zealand variants RR, GR and GP. Standardised canonical coefficients for canonical variates CV 1 and CV 2. The analysis was performed on \log_{10} transformed measurements of leaf blade characters (means and standard deviations of untransformed and transformed data given). Canonical r-squared shows the proportion of variance, in the canonical variate scores, explained by groups.

Units	Variant	n	Character Means and Standard Deviations.					Canonical r-squared (%)	
			A	B	D	E	G		
cm	RR	176	20.9 ± 11.3	12.1 ± 6.5	6.7 ± 3.8	11.1 ± 5.9	8.9 ± 4.8		
	GR	71	24.0 ± 10.2	12.9 ± 4.9	7.3 ± 3.4	12.0 ± 4.7	10.5 ± 4.6		
	GP	96	25.5 ± 10.3	16.8 ± 6.8	6.6 ± 3.1	12.9 ± 5.5	16.3 ± 7.6		
\log_{10} (cm)	RR	176	1.25 ± 0.26	1.00 ± 0.29	0.74 ± 0.3	0.98 ± 0.26	0.88 ± 0.28		
	GR	71	1.34 ± 0.18	1.08 ± 0.17	0.82 ± 0.19	1.05 ± 0.17	0.97 ± 0.21		
	GP	96	1.37 ± 0.19	1.19 ± 0.20	0.77 ± 0.22	1.07 ± 0.20	1.18 ± 0.21		
Standard canonical coefficients	CV1		-0.12	-4.4	3.9	1.4	-1.1		70.3
	CV2		2.3	-4.4	1.5	-0.7	2.1		5.1

Table 5.4 Correlations between blade characters in *C. esculenta*. These were calculated as part of a principal components analysis (SAS command PRINCOMP) of 343 observed leaves (data for taro variants RR, GR, and GP, pooled after \log_{10} transformation; analysis not presented).

	log						
	A	B	C	D	E	F	G
log D	0.92	0.94	0.94	1	0.94	0.95	0.83

5.4 Discussion

5.4.1 Taxonomy

Floral Morphology

Despite the paucity of observations on flowering, possible differences can be seen between variants RR and GP in both the absolute and relative sizes of the staminate zones and sterile appendages (Table 5.2). Variant GP, with a mean ratio of sterile appendage to staminate zone length of 0.96, may represent what Cooper (1969) regards as var. *antiquorum* (Table 5.2) despite the fact that his specimens (mean ratio = 0.90) do not fit his stated criterion of a ratio equal to or greater than one. Further, both variants RR and GP were observed in the present study to retain the sterile appendage in the terminal part of the spathe (Figure 5.5, 5.6), a stated characteristic of var. *antiquorum* (Massal and Barrau 1956; Barrau 1957; Cooper 1969). Variant RR however, with a mean ratio of sterile appendage to staminate zone length of 0.59, clearly does not fit the stated criterion for var. *antiquorum*.

Comparison of the New Zealand variants with the observations of Whitney et al. (1939; and Table 5.2) indicates that varieties in the Hawai'ian collection have, in general, a much shorter sterile appendage which is also shorter relative to the overall length of the spadix. An inflorescence of such proportions is used by Massal and Barrau (1956) to illustrate *C. esculenta* in distinction from *C. antiquorum* (Figure 5.10).²⁾

From the above it appears likely that variant RR (with a sterile appendage of large size but shorter in length than the staminate zone) is like neither *esculenta* nor *antiquorum* according to the definitions of these (as either species or varieties) by authors outside New Zealand. On the basis of flower measurements it is not clear that variant GP is of *antiquorum* kind, and it certainly is not like *esculenta*. It seems likely that Cooper (1969) attempted to apply criteria developed by previous authors working with examples which did not include flowering types similar to the New Zealand variants.

Variation in floral characters may be greater than previously indicated by their use in the identification of two varieties of *C. esculenta*, and might have future use in identifying additional varieties. Gross floral morphology may however prove no more stable or useful than vegetative characters. Further, as Plucknett (1983) points out, floral characters are often not useful as many *Colocasia* cultivars rarely flower.

General Morphology

While only leaf shape and colour appear sufficient to consistently distinguish three New Zealand variants in the field, a much greater range of vegetative characters was required by Whitney et al. (1939) to classify a large collection of varieties. A greater range of characters has not been described for the New Zealand variants as little practical benefit would result. The variants RR, GR, and GP have been described on the basis of observations over a wide range of non-cultivated habitats in a temperate climate. Descriptions made outside New Zealand generally apply to plants under various forms of cultivation in tropical climates (Whitney et al. 1939; Purseglove 1972; Plucknett 1983). These environmental differences do not allow any clear comparisons of growth habit or individual leaf characters.

Leaf shape, rather than size, has been useful in the present study for discriminating between variants. However the shapes cannot be compared usefully with previous descriptions of leaves since these are based on insufficient numbers of characters to describe shape well. Whitney et al. (1939) present only ranges of blade length and width, while Strauss et al. (1979) measure numerous characters but omit the lobe length B (or

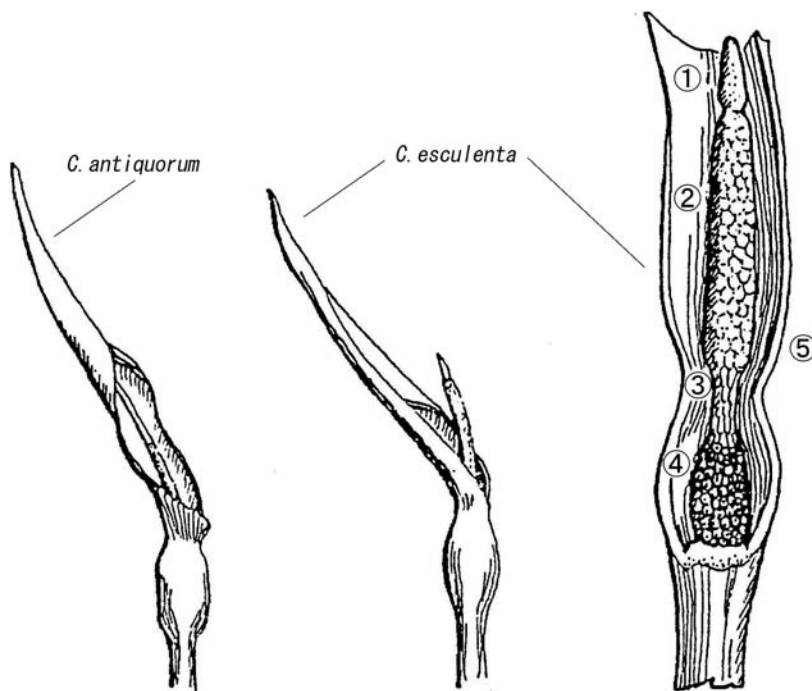


Figure 5.10 Two kinds of inflorescence in *C. esculenta*. The *esculenta* kind (right) has the following proportions: sterile appendage/staminate zone = 0.27; sterile appendage/total spadix = 0.13. Floral parts: (1) sterile appendage, (2) male flowers, (3) abortive flowers, (4) female flowers, (5) spathe cut lengthwise to show inflorescence. Illustrations and naming from Massal and Barrau (1956).

its equivalent, C) found important for best discrimination between the New Zealand variants.

In any event, leaf shape alone is insufficient to fully identify variants, cultivars, or varieties. Even comparisons using complete raw data sets and multivariate statistical techniques would probably, at best, show only very broad groupings in such an apparently polymorphic genus as *Colocasia*.

Using Field Keys for Recognition and Comparison

Classification keys based on vegetative characters, whether few or many, appear to have most use for the local recognition (for example, New Zealand or Hawai'i) of variants, cultivars, or varieties. Nevertheless, even crude comparisons between areas may be useful.

In applying the key of Whitney et al. (1939) to the New Zealand variants RR and GR, no progress could be made due to uncertainties in comparisons with corm size, production of side-corms, and petiole colour. Many variations of these characters appear in the key. However, one variety (*Aweu*) is reported with slender rhizomes which sometimes 'appear like creeping stolons' close to the surface, similar to the growth habit of variant GP. *Aweu* also resembles variant GP in leaf shape and possibly colour (Appendix 7). Although it is not possible to claim identity, the similarity may warrant an attempt to obtain living material from Hawai'i for a side-by-side comparison.

5.4.2 Natural dispersal

The distribution of taro in New Zealand is the outcome of both natural dispersal and transfer by people. The dispersal of corms and side-corms in watersheds (variants RR and GR), and by close side-shoots or spreading stolons (variant GP) has been described.

Cooper (1969), summing up observations of seven spadices from New Zealand sources (variants not identifiable), notes that they have small fruit and white ovules when fresh, but when spathes and stalks wither the fruit fail to ripen seed. Similar observations were made during the summer of 1982–83 for both variants RR and GP. All observations made to date indicate that there is no seed production in New Zealand.

The records of flowering in winter and summer suggest that seasonal control of flowering is poor, though this may differ for different variants. The number of records suggests that flowering is quite common.

Outside New Zealand, seedlings or germinating taro seed have not been observed in areas where the crop is cultivated and it is generally believed that seed rarely or never germinate.³ Seedlings if formed may perish due to fungal attacks or damping off (Sunell and Arditti 1983). Seed have germinated under a wide variety of controlled conditions (Ghani 1982; Strauss 1983; Sunell and Arditti 1983). Seed production after artificial self-pollination varied from much to little in different varieties (Sunell and Arditti 1983). Mass flowering may be a general characteristic of stolon-producing *Colocasia* such as variant GP, since Wilson (1982) notes from casual observations that natural flowering in *Colocasia* appears associated with a tendency towards stolon production.

5.4.3 Archaeology

Finally, good and bad news for archaeologists: taro pollen certainly is produced in New Zealand swamp sites but apparently, in Highland Papua New Guinea, it has proved impossible or extremely difficult to distinguish claimed fossil taro pollen from the pollen of other genera (Spriggs 1982). Encouragingly, the seed is hard and may have useful diagnostic characters. It remains to be tested how easily the seed rots.

5.5 Conclusion

Three major variants of New Zealand taro are readily recognised in the field. These have only been informally named as variants in order to stress that nothing should be assumed about their phylogenetic relationships. The taxonomic descriptions that have been made here, and elsewhere, are inadequate for positive identification of genetically similar taro outside New Zealand.

The present field observations indicate that taro is readily able to survive and self-propagate vegetatively in New Zealand, without human intervention.

Notes

- 1) Not all attempts to analyse chromosomes were successful. The standard method — described in Appendix 10 — works best when the plants are growing rapidly, eg. in warm conditions with increasing day-length. For tropical cultivars, the day length condition may not be important.
- 2) While describing a new species of *Colocasia* in Borneo, Hay (1996) provides a useful review of the naming of *C. esculenta* and its varieties.
- 3) A first indication that this view is wrong was provided by Barrau (1959), who found wild taro with fruit and seeds in Papua New Guinea. See also Figure 9.3, this volume.

Chapter Six Cytology

6.1 Introduction

Here, the chromosome numbers of New Zealand taro are investigated and the observations of previous authors are confirmed. The variants identified on morphological grounds (Chapter Five) are characterised further by chromosome number and karyotype. Observation of the karyotypes provides a further means for distinguishing the variants and allows limited speculation about the evolution of the nuclear genomes.

Rattenbury (1956, 1957) reported the somatic cell chromosome number of $2n = 42$ for untended taro from the Cavalli Islands. Further counts made by Rattenbury for New Zealand taro were reported by Yen and Wheeler (1968). ‘Apparently wild’ taro from Great Barrier Island and Spirits Bay also gave counts of $2n = 42$, and the specimen from Great Barrier Island was morphologically similar to that from the Cavallis (Yen and Wheeler 1968). A variety cultivated by the Māori of Northland, and called ‘island taro’, shared some morphological likenesses as well as the 42-chromosome complement with a wild specimen called *taro hoia* in the same area. Two other cultivated varieties from this district called *makatiti* and *pongu* gave counts of $2n = 28$. A reputedly Chinese variety grown by a Chinese market gardener in Auckland had the same chromosome number ($2n = 42$, implied by Yen and Wheeler 1968) as morphologically identical plants collected from two untended situations near Māori settlements in North Auckland and the Bay of Plenty. In their Pacific-wide study, ‘no obvious morphological correlates were noted in the field during the periods of collection or during the experimental growing in New Zealand of varieties of known chromosome number’ (Yen and Wheeler 1968).

As a consequence of the confusion surrounding the Linnaean nomenclature of *Colocasia* species and varieties, little significance can be placed on the correspondence between reported species/variety and chromosome number in lists such as presented by Plucknett et al. (1970), Marchant (1971), and Ramachandran (1978). In a particular instance, Rattenbury (1957) reported the New Zealand chromosome number under the name *C. antiquorum* Schott, while both he (Rattenbury 1956) and Yen and Wheeler (1968) regarded this name as synonymous with *C. esculenta* (L.) Schott, the name used by the latter authors when reporting the New Zealand chromosome numbers.

As part of a stated attempt to resolve conflicting results among chromosome studies of the Araceae, Marchant (1971), noted the range of counts previously reported for *C. antiquorum* (L.) Schott. Summarily, and without discussion, *C. antiquorum* is identified as a hexaploid ($2n = 42$) and *C. esculenta* as diploid [sic] ($2n = 28$), both with a basic number of $x = 7$.

Given the confused state of affairs outlined, I will simply present here all the previously reported $2n$ chromosome numbers under the genus name *Colocasia* Schott. The reports may be found cited in the lists of Plucknett et al. (1970), Marchant (1971) and Ramachandran (1978). Chromosome numbers reported for *Colocasia* Schott are $2n = 14, 22, 26, 28, 36, 38,$ and 42 . Darlington and Wylie (1955) also report counts of $2n = 24$ and 48 . For the Pacific region, from Japan through Southeast Asia and out to Eastern Polynesia, Yen and Wheeler (1968) report only $2n = 28$ and 42 .

Two polyploid number series have been recognised for *Colocasia*, founded on the basic chromosome numbers $x = 12$, and $x = 7$ or 14 . Although Mookerjea (1955) reports an individual with $2n = 14$ as a probable diploid, that is with a basic number of $x = 7$, Yen and Wheeler (1968) note as an alternative explanation that Mookerjea's find may be a rare natural haploid. However, Plucknett et al. (1970), citing Sharma (1956), list a count of $2n = 14$ for a hybrid plant, thus implying a diploid with the basic number of $x = 7$. More recent authors also differ in what they regard as the basic chromosome number for the $2n = 28$ and 42 series. Marchant (1971) gives the basic number as $x = 7$, while Purseglove (1972) regards it as $x = 14$. Ramachandran's report (1978) of irregular meiotic pairing behaviour in pollen mother cells is good evidence of triploidy in a variety with 42 chromosomes. It seems quite possible that in fact both $x = 7$ and $x = 14$ occur as basic chromosome numbers in the genus *Colocasia*.¹⁾

6.2 Materials and Methods

All plants investigated were obtained from within New Zealand. Material used for cytological analysis came from potted plants of the living plant collection in Auckland. Shoots were removed from the pots and stripped of leaves and roots before export to Australia, where the investigation was made. The shoots were repotted in a loam and peat potting mix and grown in a glasshouse at the Research School of Biological Sciences, Australian National University, Canberra. Root tips 1–2 cm long were harvested from young roots 1–10 cm long, 1–2 weeks after repotting, at times during morning or afternoon.

Pre-treatment, fixation, staining, and squash of root tips were performed as described in Appendix 10. Feulgen staining, using a modified formula after Darlington and La Cour (1969) was followed by lacto-propionic orcein.

Chromosome counts of cells at mitotic metaphase, and photographs, were made using a Zeiss photomicroscope with either a Neofluar 100x/1.3 aperture/oil immersion objective for bright field optics or a Ph 3 oil immersion lens for phase-contrast. Photographs were taken with green light on panchromatic, black and white film rated at ASA 25 for bright field exposure and ASA 15 for phase-contrast. Varying magnification was used depending on the spread of chromosomes on the slide. For the preparation of karyotypes enlargements of photomicrographs were traced, the tracings enlarged and then reduced to similar scale by Xerox. Chromosome outlines were cut out, sorted, and retraced. Sorting was carried out by the following routine: outlines were first sized against two ruled divergent lines, then roughly grouped according to centromere position.

Closer matching was then made largely on the basis of shape and centromere position as judged subjectively by eye. Grouping by centromere position followed the definitions provided by Dyer (1979) for median centromeres (arm length ratio 1:1), sub-median (arm ratio $> 1:1$, $< 3:1$), and sub-terminal (arm ratio 3:1 or greater). Since accurate and repeated measurements are lacking, the groupings must be regarded only as approximate and tentative. Other terminology used follows Dyer (1979).

6.3 Observations

Details of reliably observed chromosome counts are presented in Appendix 10. Somatic cell chromosome counts were all $2n = 42$ for the variants RR, GR, and GP, represented by plants from sites spanning the distributional ranges (Chapter Seven) of each of these variants (Figure 6.1; Appendix 10). Two accessions of variants known only from single sites have the number $2n = 28$ (AKL 34 and AKL 79, Figure 6.1). Unreliable counts previously made by the author in Auckland also indicated the number $2n = 42$ for variant RR (accessions AKL 2, 50, 84, and 86), variant GR (AKL 67), and variant GP (AKL 25 and 29).

Outline drawings for the karyotypes of variants RR, GR, GP, AKL 34, and AKL 79 are presented in Figure 6.2. Two examples of each are given, with the chromosomes grouped according to centromere position, size, and general shape. Features of the karyotypes of each variant are outlined below. Note that where little size range is apparent within a numbered group, allocation to pairs as shown in Figure 6.2 is highly speculative.

6.3.1 Variants RR and GR

Chromosomes with sub-terminal centromeres: (1) Three pairs of larger chromosomes. A slight range of size between pairs. (2) Three pairs of smaller chromosomes, centromeres approaching sub-median position. A slight range of size between pairs.

Chromosomes with sub-median centromeres: (3) Three pairs of larger chromosomes, centromeres approaching sub-terminal position. Some range in size apparent between pairs. (4) Three pairs of larger chromosomes, similar in size to group three. No obvious range in size. (5) Three pairs of smaller chromosomes. No obvious range in size. (6) Three pairs of chromosomes smaller than those in group five. No obvious range in size.

Chromosomes with median centromeres: (7) Three pairs with possibly a slight range in size.

6.3.2 Variant GP

Chromosomes with sub-terminal centromeres: (1) Three unpaired chromosomes ranging in size.

Chromosomes with sub-median centromeres: (2) Three unpaired chromosomes with centromeres approaching sub-terminal position. No obvious range in size. (3)–(7) Five groups of six chromosomes, with groups ranging in size from large to small. No obvious range in size within groups.

Chromosomes with median centromeres: (8) Three pairs with no obvious range in size.

6.3.3 Variants AKL 34 and AXL 79

Chromosomes with sub-median centromeres: (1)–(6) Six groups of four chromosomes, with groups ranging in size from large to small. No obvious size range within groups.

Chromosomes with median centromeres: (7) Two pairs of chromosomes with possibly a slight difference in size.

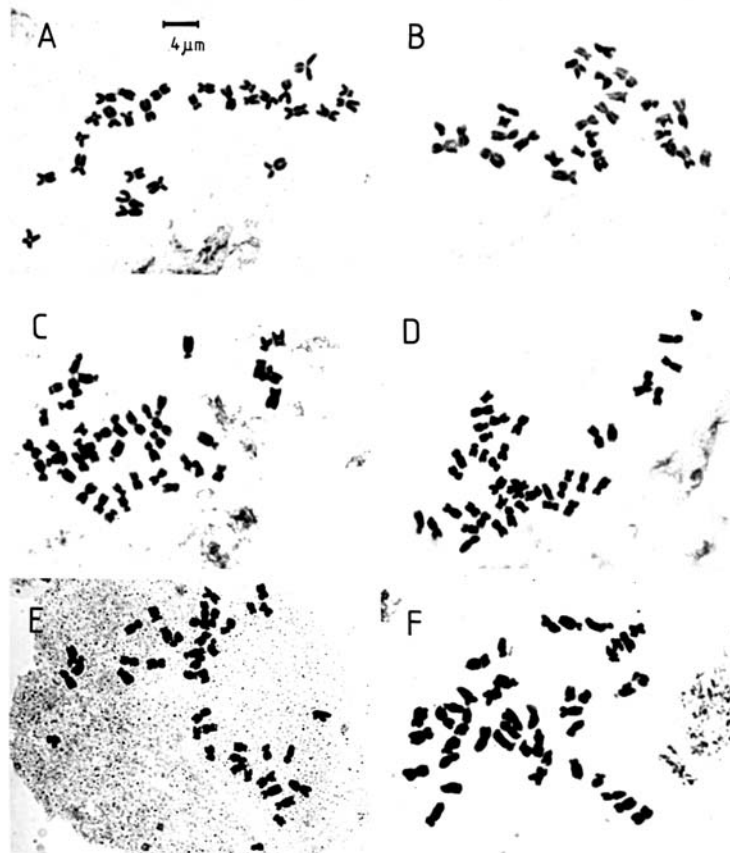


Figure 6.1 *C. esculenta*–root-tip metaphase chromosomes from single cells of: (A) AKL 34, $2n=28$; (B) AKL 79, $2n=28$; (C) Variant GR, AKL 83, $2n = 42$ (photo collage); (D) Variant GP, AKL 30, $2n = 42$; (E) Variant RR, AKL 48, $2n = 42$; (F) Variant RR, AKL 27, $2n = 42$. Scale: highly approximate, for A–E.

Centromere	Colocasia	esculenta	AKL 49 Variant GR
sub-terminal			
sub-medium			
median			

Centromere	Colocasia	esculenta	AKL 83 Variant GR
sub-terminal			
sub-medium			
median			

Centromere	Colocasia	esculenta	AKL 17 Variant GP
sub-terminal		sub-medium	
sub-medium			
median			

Centromere	Colocasia	esculenta	AKL 30 Variant GP
sub-terminal		sub-medium	
sub-medium			
median			

Centromere	Colocasia	esculenta	AKL 34 cell 1
sub-medium			
median			

Centromere	Colocasia	esculenta	AKL 34 cell 2
sub-medium			
median			

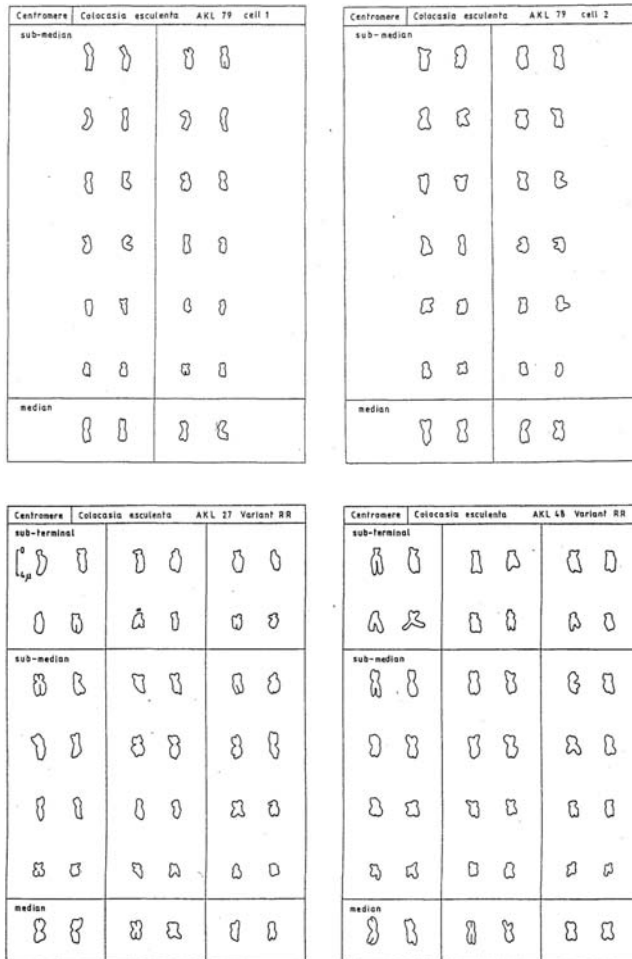


Figure 6.2 Tentative karyotypes of five variants of New Zealand taro. Variant RR: $2n = 42$ (accessions AKL 27 and 48); Variant GR: $2n = 42$ (accessions AKL 69 and 83); Variant GP: $2n = 42$ (accessions AKL 17 and 30). Variant AKL 34: $2n = 28$ (two cells from one root tip); Variant AKL 79: $2n = 28$ (two cells from one root tip). Scale similar but not identical for each accession. A highly approximate indication of scale is shown for AKL 27.

6.4 Concluding Discussion

6.4.1 Chromosome numbers

The repeated observation of the chromosome number $2n = 42$ has firmly established this as a characteristic of each of the three variants RR, GR, and GP. The observations also confirm the previous reports of $2n = 42$ for taro at Spirits Bay, the Cavalli Islands, Great Barrier Island, North Auckland, and the Bay of Plenty. In contrast to the report of Yen and Wheeler (1968), no taro with the number $2n = 28$ were observed in accessions from in or around Māori communities of Northland. However, the variant AKL 34 ($2n = 28$) is said to have arrived at its present single known site in Whangarei hand-to-hand from a Māori source in the central inland Bay of Islands (K. Reynolds pers. comm. 1981, 1982; T. Chamberlain pers. comm. 1982). The variant AKL 79 ($2n = 28$) is also known from a Māori source (M. Rau-Kupa pers. comm. 1983), but in Taranaki. This is an area where no field exploration has been made, and from where other as yet untested variants (AKL 80, 81, and 82) have been received.

6.4.2 Karyotypes

Variants RR and GR

Initial observation of karyotypes in the tentatively proposed arrangement shown in Figure 6.2 indicates that the variants RR and GR are similar. One possible interpretation of the arrangement, assuming variation along rows (Figure 6.2) between chromosome pairs, is that it represents an amphidiploid allohexaploid ($2n = 6x = 42$) of a form such as AABBCC. The possible routes of origin for such a combination of genomes are varied and complex, and do not warrant discussion here in the absence of a definite karyotype.

Variant GP

While the karyotypes of variants RR and GR quite clearly suggest a basic chromosome number of $x = 7$, the karyotype of GP may reflect a basic number of $x = 14$. Although in variant GP few distinctions are apparent among the large number of sub-median chromosomes, the presence of three unpaired sub-terminal chromosomes of varying size could reflect an allotriploid arrangement ($2n = 3x = 42$) of the form ABC. A basic number of $x = 14$ could have evolved by differentiation between pairs of homologous complements of $x = 7$ present in an amphidiploid allopolyploid ancestor (for example AABBCC, AABB) or autotetraploid ancestors (for example AAAA); or between the diploid genomes ($2n = 2x = 14$) of different ancestral parent populations prior to hybridisation events and amphidiploidy. The degree to which such differentiated complements $x = 7$ might behave in non-homologous fashion would be an important determinant of chromosome pairing behaviour during meiosis.²⁾

It is unfortunate that reports of seed production and germination have not generally been accompanied by the observation of karyotypes or chromosome number (for example, Strauss et al. 1980; Ghani 1982; Shaw 1982). It can only be hoped that in future, greater attention will be given to combining observations of cytology with breeding trials and observations of natural seed production.

Approximately 2500 seed per inflorescence were harvested by Strauss et al. (1980) after hand pollination of *C. escutenta* var. *antiquorum* cv. UCI Runner, grown under greenhouse conditions.

Mookerjea (1955) describes an Indian 42-chromosome karyotype, but the absence of a clear pictorial presentation prevents useful comparison.

Secondary constrictions and chromosome satellites observed by Mookerjea (1955) may or not be present in the New Zealand karyotypes. The observations made so far are insufficient for further comment on the potential of constrictions and satellites as genomic markers.

Other Variants

The karyotypes of AKL 34 and AKL 79 appear similar, with a possible arrangement of 28 chromosomes into seven groups of four indicating a basic number of $x = 7$. The uniformity within each of the seven groups suggests an autotetraploid arrangement of the form AAAA.

However, in the absence of any knowledge of intrachromosomal structure or meiotic pairing behaviour, allotetraploid (AABB) or even diploid ($2n = 2x = 28$) arrangements must be regarded as possible interpretations. The regular meiosis and high pollen fertility reported by Ramachandran (1978) for two South Indian 28-chromosome varieties could reflect either amphidiploid tetraploid (AABB) behaviour, or the fertility of a non-hybrid diploid (AA) (Dyer 1979). Thus Ramachandran's interpretation of the South Indian varieties as diploid ($2n = 2x = 28$) must be treated as tentative. This example illustrates the caution required should further study of the New Zealand variants be made.

6.4.3 Cytological correlations with phenotypes

An interesting aspect of the present observations is that there seems to be a correlation between morphological phenotype and karyotype. Variants RR and GR, of similar growth habit, share similar karyotypes, while variant GP is dissimilar in both growth habit and karyotype. Variants AKL 34 and 79 share a third kind of growth habit and a third form of karyotype. It would be of considerable evolutionary interest to verify this suggestion with both the present variants and a wider selection of cultivars and wild forms. Verification would require better definitions than are presently available for both phenotypes and karyotypes.

The observation of marked morphological differences between the variants, RR, GR, and GP, all with the chromosome number $2n = 42$, confirms the lack of correlation between morphology and chromosome number, as noted by Yen and Wheeler (1968).

6.4.4 Future investigation

Future investigation of meiotic pairing behaviour is possible for at least the variants RR and GP, since both of these have been observed flowering quite commonly (Table 5.1). During the formation of pollen, varying genomic arrangements may result in similar meiotic pairing behaviour, so observation of meiosis should be accompanied by the investigation of intrachromosomal structure. This is needed to test for variation between

putatively identical genomes, or for homologies between putatively dissimilar genomes.

A large range of techniques are available for such an investigation including, in addition to the traditional cytological stains: Geimsa stain, DNA-specific fluorescent dyes, and radioactive DNA probes made from cloned genes or fragments of genes (see Chapter Twelve).

Notes

- 1) Cusimano et al. (2012) demonstrate that $2n = 28$ is the common diploid number for genus *Colocasia*, and that the ancestral haploid chromosome number for Araceae is $n = 16$, with chromosome loss leading to the haploid number $n = 14$.
- 2) The discussion up to here follows the observed variation in karyotypes. In the original MSc thesis, discussion continued based on a misidentification of fruit and seeds (which suggested that var. GP was a fertile hexaploid, not a sterile triploid). A recent study by Cusimano et al. (2012) indicates that a haploid chromosome of $n = 9$ is ancestral deep in the evolutionary past of all Araceae, that this doubled to $n = 18$ in early history of Araceae, and that a haploid chromosome number of $n = 14$ (diploid number of $2n = 28$) arose by reduction among distant ancestors of the genus *Colocasia*, within the Araceae (these authors reject the use of 'x' basic number terminology).

Chapter Seven Distribution

7.1 Introduction

Observations are presented here from fieldwork conducted in 1982 and 1983. Intensive fieldwork was carried out in widely separate areas of the North Island, establishing something of both the general range and local distribution pattern of the three taro variants already described (Chapter Five). In order to gain insight into the possible historical basis of distribution, records also were made of cultural practices related to taro.

The observations provide limited and circumstantial evidence of when taro introductions to New Zealand may have been made. Consideration is given to the possibility, raised by Rattenbury (1956) and Yen and Wheeler (1968), that taro present on the Cavalli Islands, at Spirits Bay, and on Great Barrier Island are remnants from pre-European times.

Early written records indicate that taro was once widespread in Māori cultivations of the North Island (Nicholas 1817; Wade 1842; Best 1976). In 1769, Captain Cook and his companions observed taro in plantations around the East Cape and in the Bay of Islands (Best 1976). Colenso (1880) listed Māori names for taro in two groups, according to the geographic origin of each name:

- (1) the North, including the Bay of Islands, Hokianga, and Kaitaia districts; and
- (2) Hawkes Bay and the East Coast, south of East Cape.

European crops in Māori cultivations were commonly observed by the early writers after Captain Cook. Hargreaves (1959) stated that by the time the first European settlers arrived in the North Island (between 1800 and 1850), Māori agriculture had developed to such an extent that it was able to provide the settlers with regular supplies of pigs, and crops of European origin: potatoes, maize, and wheat.

Taro appears to have been quickly displaced after the introduction of European crop plants. Cheeseman (1900) notes that fifty years previously ‘taro was seen in every Māori cultivation of any size’ but had by 1900 fallen into almost total disuse. Kirk (1868) briefly described, amongst naturalised plants of the Auckland Province, ‘*Colocasia antiquorum*’ as remnant or escaped from field cultivation, found growing on waste places or by roadsides, and in wet soil or water.

Taro also was observed last century in South Island cultivations. Dieffenbach (1843) found taro growing alongside potatoes by the village of Mokupeka, on Arapawa Island, Queen Charlotte Sound, about 1839, while Brunner (1952) observed taro plantations ‘of former days’ near a deserted *paa* (hill forts) at the mouth of the Hokitika River, in 1847. It is not clear from these and other reports whether taro was a pre-European crop in the

South Island.

A fuller outline of records and events during the early period of European contact is presented by Leach (1984).

Details of site location, or descriptions which allow direct identification of variants, have not generally been presented. Recently, taro chromosome numbers were reported for unspecified sites on the Cavalli Islands (Rattenbury 1956, 1957), Great Barrier Island, Spirits Bay and near settlements (unspecified) of Northland and the Bay of Plenty (Yen and Wheeler 1968).

Hayward et al. (1979) did report specific locations for taro sites seen during an archaeological survey of Motukawanui Island of the Cavalli's group.

7.2 Methods

7.2.1 Botanical exploration: strategy

Because of cost and time limitations, fieldwork was conducted in areas where taro was already known to exist. Initial information came from correspondence (Appendix 1), site records of the New Zealand Archaeological Association, historical references, and through personal contacts with a number of archaeological and botanical fieldworkers.

In an exploratory field trip (Matthews 1982b) it appeared that taro was common in rural Māori communities. Subsequent field surveys were generally directed through such communities.

Surveys were made by observation from the road, interviewing farmers and other residents, and exploration by foot. Taro sites were recorded on archaeological site record forms of the New Zealand Archaeological Association (Appendix 2). These provided a convenient recording format. Map grid references were obtained from maps of the NZMS 1, one inch to the mile, series. The new NZMS 260 metric map series was not used as its coverage was incomplete.

7.2.2 Cultural observations

Observations and information on cultural practices were recorded as opportunity arose, and depending on the inclination and knowledge of informants.

7.2.3 Coverage

During field survey, coverage of local areas was never complete. The subjective decision to leave a locality was made when either it was felt that too little new information could be obtained by interview or observation, or when the effort of finding people or visiting possible sites was too time-consuming.

A limited knowledge of local absences of taro was obtained in interviews with farmers familiar with large areas of land, or with people familiar with a local community. Constraints on time were exerted by the day-to-day necessities of living and by the overall time allotted to the field trip. Legal restraints on access also limited observation.

Because of these limitations on coverage in the field, only the known positive extent of distribution can be presented here.

7.3 Observations

7.3.1 Taro sites

For areas and dates of fieldwork (1981–1983), see Chapter Five.

Records and definitions of site categories

The records of sites are filed in the Department of Botany Herbarium, University of Auckland, and a duplicate set is held at the Auckland office of the New Zealand Archaeological Association. A list of the sites with tabulated descriptions is presented in Appendix 2 and summarised here in Table 7.1. Explanations of the terms used are as follows:

Botany Department (B.D.) Site Number Map Number for the N.Z.M.S. 1 map series (unless otherwise indicated) followed by a serial number for each site.

Variant Botanical variants (informal nomenclature, see Chapter Five) found at each site.

Cultivated Garden The plants are found in soil which is presently cultivated. Plants may or may not form a clumped growth habit depending on the attention given to them.

Non-cultivated Garden The plants are found in soil which is not presently cultivated. Plants of each of the variants typically form clumps by natural vegetative propagation. Varying intervention in the natural growth of the plants may occur depending on how people use them.

While cultivation of the soil clearly identifies a garden, non-cultivation may make it difficult to identify the plants as a garden component rather than as wild plants. If information from a local resident is not available, two kinds of circumstantial evidence can indicate plants as a non-cultivated garden component: (1) the immediate proximity of structural evidence for human settlement (house or other building of the European architectural tradition), and (2) the presence of other exotic plants characteristic of gardens: for example, the garden ornamentals *Alocasia macrorrhizos* (elephant's ear) and *Zantedeschia aethiopica* (arum lily).

Non-derelict: non-cultivated garden sites are considered non-derelict if they are in the immediate proximity of an inhabited or clearly habitable house.

Derelict: non-cultivated garden sites are considered derelict if they are in the immediate proximity of only ruined or clearly uninhabitable structures, or are apparently garden sites only because of the presence of other exotic plants.

Wild: Non-cultivated plants are classed as wild if no evidence of settlement (of European design) is seen or visible in the immediate proximity. Non-cultivated plants are also classed as wild if the circumstantial evidence of association with settlement (of European design) seems unclear. This requires subjective evaluation of the field evidence, so that the site categories of 'non-cultivated garden' and 'wild' overlap to an unmeasurable extent.

This classification of sites depends upon the thoroughness of field exploration, which for practical reasons can never be complete and consistent. Relevant field evidence of settlement also may have been destroyed.

Criteria for recording sites as separate

Generally, each site-record represents taro in a local watershed (stream, gully, rivulet, etc.) separate from other local watersheds. Exceptions to this rule were sometimes made where taro in a larger confluence is found below taro in a tributary or tributaries some distance away. A site on the larger confluence is separately recorded in this situation because it is not possible to identify a particular tributary as the only likely upstream source of taro (because more than one tributary is known with taro, or because not all the tributaries have been searched). Exceptions to the rule also were made where taro were found near each other, but in different site environments.

Non-cultivated and cultivated taro near a house may be recorded as separate sites if one group does not appear immediately derived from the other.

Summary of site records

A total of 300 sites were recorded in the file, including 243 sites reported by the present author. Three sites containing only taro other than the variants RR, GR, and GP are not represented in the summary (Table 7.1). The distributions of variants other than variants RR, GR, and GP (AKL 34, AKL 79, AKL 80, AKL 81, AKL 82, and AKL 87) are limited to single sites and are not considered further here.

The oldest site recorded was observed in 1930 or 1931 (N41/1), and the oldest site seen again in the present study was first recorded twenty-six years previously, in 1957 (N70/4, with variant GP).

The majority of sites recorded before 1981, and of sites recently observed only by persons other than the author, fall in the 'not known' categories shown in Table 7.1. Because of this, the frequencies of identified variants and of known site description largely represent the present-day distribution of taro.

Photographs of sites in each of the categories defined for site description are shown in Figures 7.1 and 7.2.

Geographic distribution of *C. esculenta* variants

The distribution of the three variants RR, GR, and GP in the areas of intensive fieldwork (Figure 7.3) are shown in Figures 7.4, 7.5, and 7.6. These areas are North Auckland, the Hauraki Gulf, and East Cape, and represent respectively the northern, middle, and southern areas of the explored distribution range. Inland East Cape (Figure 7.6) was not searched since it is largely uninhabited, unroaded, steep hill-country, rising to the Raukumara Ranges.

Other areas which are known through correspondence and archaeological site records to have taro have not been explored. These areas are the Kaipara Harbour district, Tauranga, Taranaki, and the northern West Coast of the South Island.

The South Island distribution does not seem likely to be important (J. Eyles pers. comm. 1982; G. Walls pers. comm. 1982), and A. Sheward (pers. comm. 1984) reports no success at finding 'pre-European' taro in the western Waikato area.

The northern and southern extremes of observed distribution are shown in Table 7.2 for each of the three major variants. Variant RR was overall the most commonly found,

Table 7.1 Occurrence of *C. esculenta* variants RR, GR, and GP in different site categories

VARIANT	SITE DESCRIPTION					Total	% Known Variants
	Garden			Not Known			
	Cultiv.	Non-cultivated					
	Non-derelict	Derelict	Wild				
RR	21	49	12	55	28	165	75
GR	1	18	1	6	2	28	13
GP	0	3	1	21	2	27	12
Not Known	2	1	2	8	76	89	
TOTAL	24	71	16	90	108	309	
Corrected Total	23	65	16	85	108	297	
Known Sites (%)	12	34.5	8.5	45			100

Note¹: site numbers corrected to account for twelve sites where two variants were recorded within each site.

Table 7.2 Observed ranges of *C. esculenta* variants RR, GR, and GP

		longitude	latitude
Variant RR	N	172°53'	34°28'
	S	175°00'	39°20'
Variant GR	N	172°52'	34°26'
	S	178°22'	37°40'
Variant GP	N	172°52'	34°23'
	S	177°37'	37°49'

while variants GR and GP were found with almost equal, lower frequency (Table 7.1). In all areas searched, variant RR predominated in frequency, while variants GR and GP appeared largely restricted to the Northland area. Variant GR is also known from one site close to the southern head of the Hokianga Harbour, but not shown in Figure 7.4, and variant GP is known from one site at the southern head of the Manukau Harbour, South Auckland, not shown in the figures. Variant RR was also the most common variant found with scattered observations outside the areas of intensive fieldwork.

The local distributions of taro (variant RR) on two offshore islands, North Auckland, are shown in Figures 7.7 and 7.8. These correspond to two of the three clusters of sites indicated in Figure 7.4.

The first cluster indicated in Figure 7.4, northeast of Tauroa Point, consists of eight recorded sites. These may be derived from at least four different plantings in the presently forested tributaries of two farmed valleys, above what was once the Whangatane swamp. Four of the recorded sites contain variant RR; the other sites were not visited but were reported by the farmer.



Figure 7.1 *C. esculenta* sites, North Island, New Zealand.

Above: Variant GP growing wild at Ngawha, Bay of Islands (site N15/4) May 1982.

Lower: Kikipaku Stream on Motukawanui, of the Cavalli Islands, Northland (site N8/12). December 1982. Established plants and loose corms of variant RR were found wild and scattered along the streambed, which was dry at the time of visit. This site was previously recorded by Hayward et al. (1979) for taro downstream (towards left of photo) from the upper region shown here.



Figure 7.1 cont'd.

Variant RR (centre) cultivated in a mixed-crop, family garden at Waima, southern Hokianga (site NI4/17). February 1983. Other crops are, from left: *Zea mays* (corn), *Solanum tuberosum* (potato), and at immediate right of the taro: *Ipomoea batatas* (kumara). Māori gardens of similar composition were recorded early in the nineteenth century.



Figure 7.2 Further sites with *C. esculenta*, North Island, New Zealand. *Upper left*: Variant RR (arrow), wild, mixed with *Alocasia* sp. (see Figure 2.1). Plants reaching 1–2 metres height, growing on a supralittoral beach flat, by the outlet of a small stream. Near Te Kaha, East Cape (site N61&60/5). January 1983. *Upper right*: Variant RR, wild. Clumps in and beside a stream. The patch is about ten years old, according to the farm owner who originally transferred plants here from Motairehe nearby. Northern Great Barrier Island, Hauraki Gulf (site NZMS 259/6). January 1983. *Middle left*: Variant RR, wild. Clumps in level area beside a small stream. This patch is a locally recognised source of food, and evidence was found of very recent harvesting of corms. Tikitiki, East Cape (site N72/5). January 1983. *Middle right*: Variant RR, in derelict, non-cultivated garden (now paddock). Stunted plants in hard, dry ground. Tikitiki, East Cape (site N72/4). January 1983. *Lower left*: Variant RR, in non-derelict, non-cultivated garden. Plants formerly in the backyard of the house were dug up and thrown over the fence, and now survive in the adjacent ditch. The source of the plants isn't known in the homeowner's family history, but they were possibly brought here as long ago as 1902, when the house was built. Port Charles, Coromandel Peninsula, Hauraki Gulf (site N35/1). August 1983. *Lower right*: Variant GP, in non-derelict, non-cultivated garden. Plants reaching between 1 and 2 metres height, shaded, in a boggy ditch adjacent to a house. Southern Hokianga, Northland (site N14/14). February 1983.

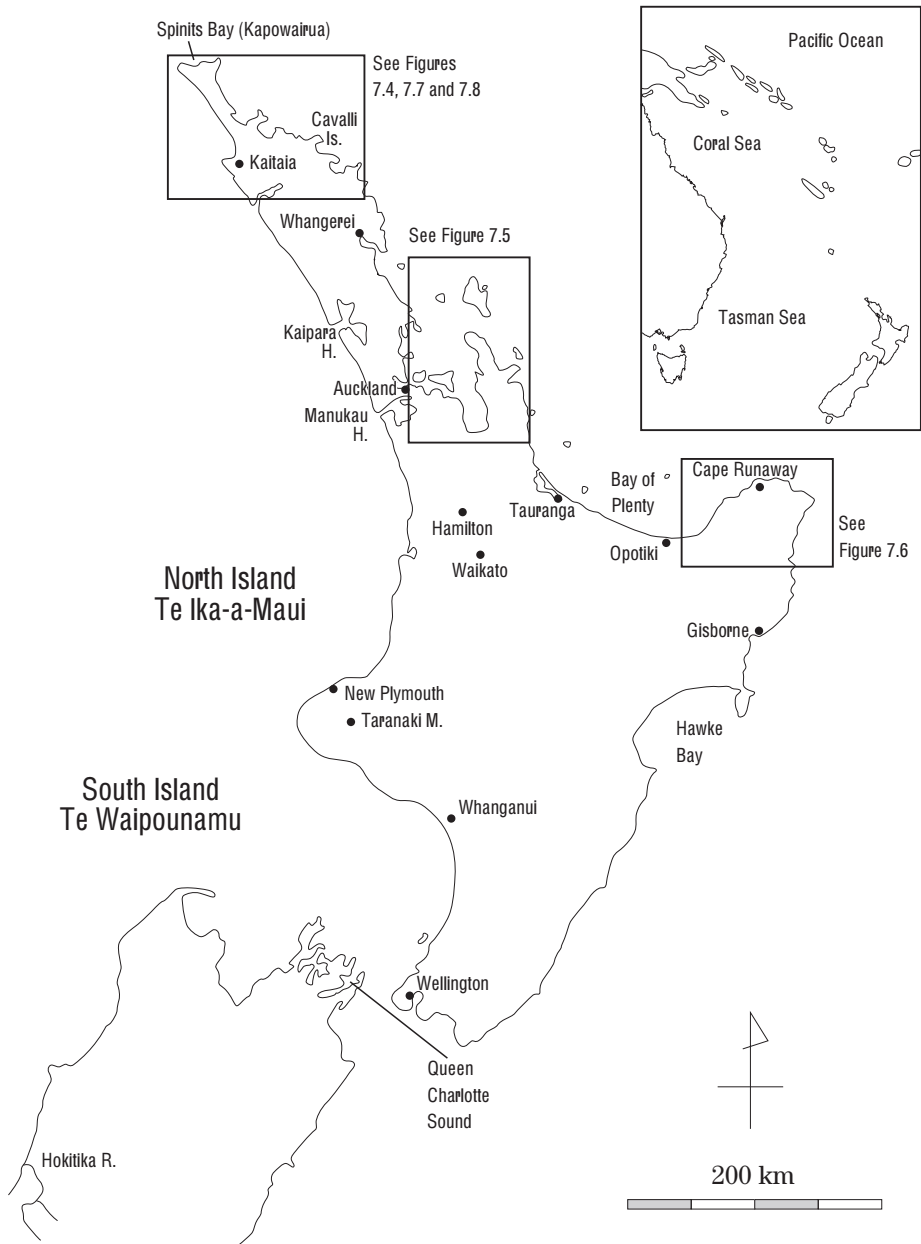


Figure 7.3 New Zealand locations mentioned in text, and areas of intensive fieldwork (rectangles)

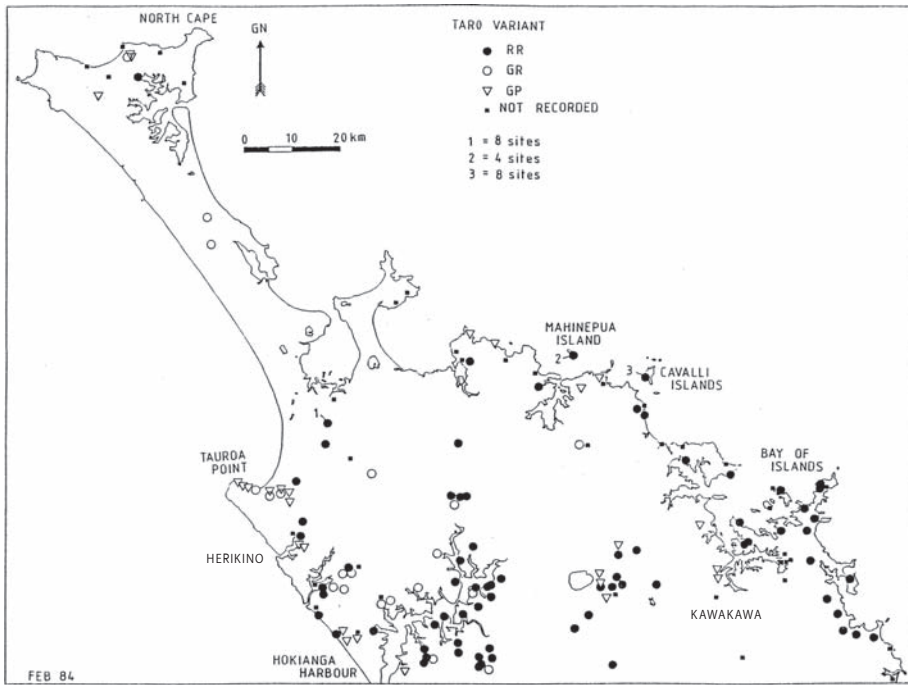


Figure 7.4 *C. esculenta* in Northland: observed distributions of variants RR, GR, and GP. Site clusters 2 and 3 are shown in Figures 7.7 and 7.8 respectively.

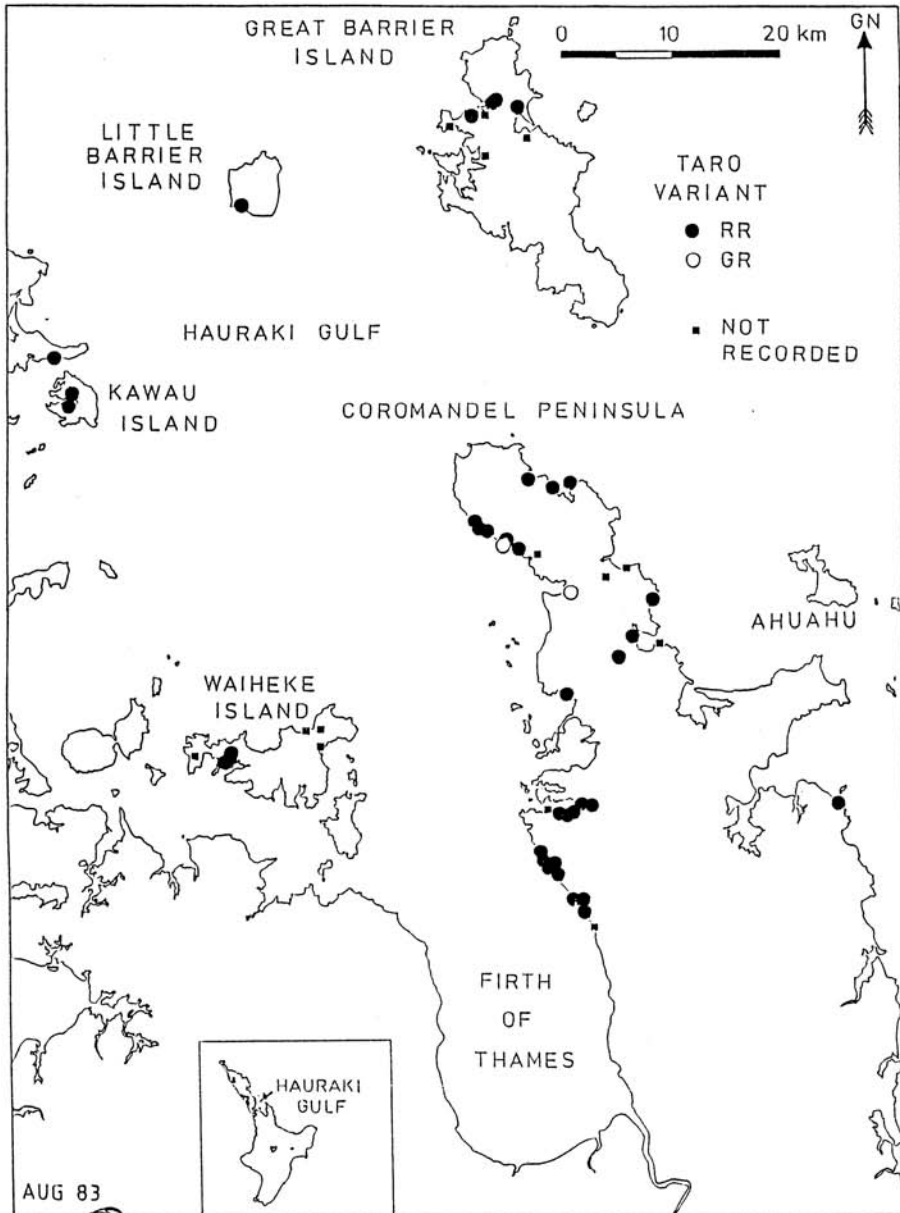


Figure 7.5 *C. esculenta* in or near the Hauraki Gulf, Auckland: observed distributions of variants RR and GR. Variant GP has not been observed here

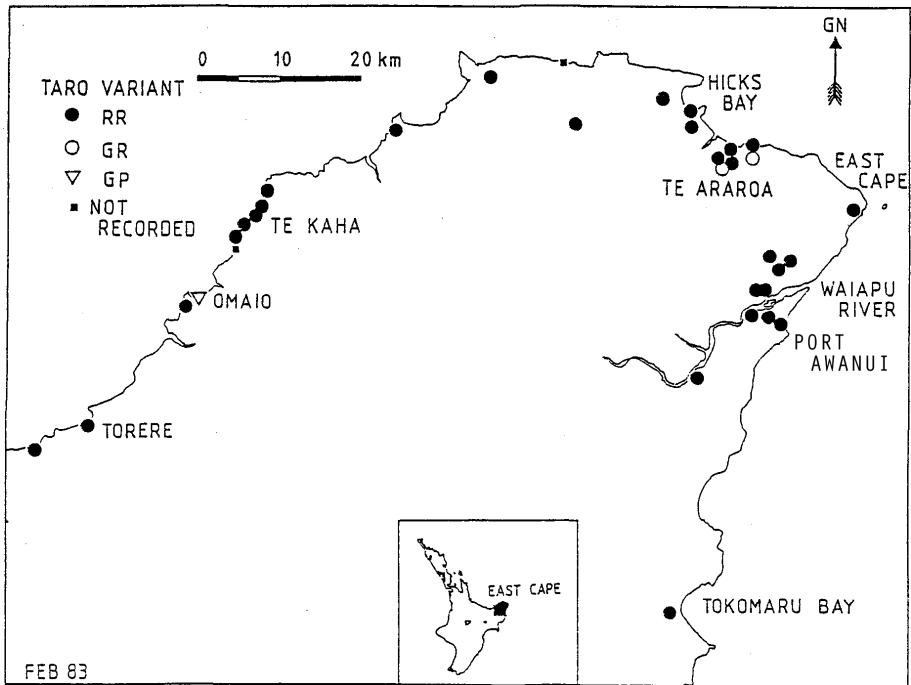


Figure 7.6 *C. esculenta* around East Cape: observed distributions of variants RR, GR, and GP

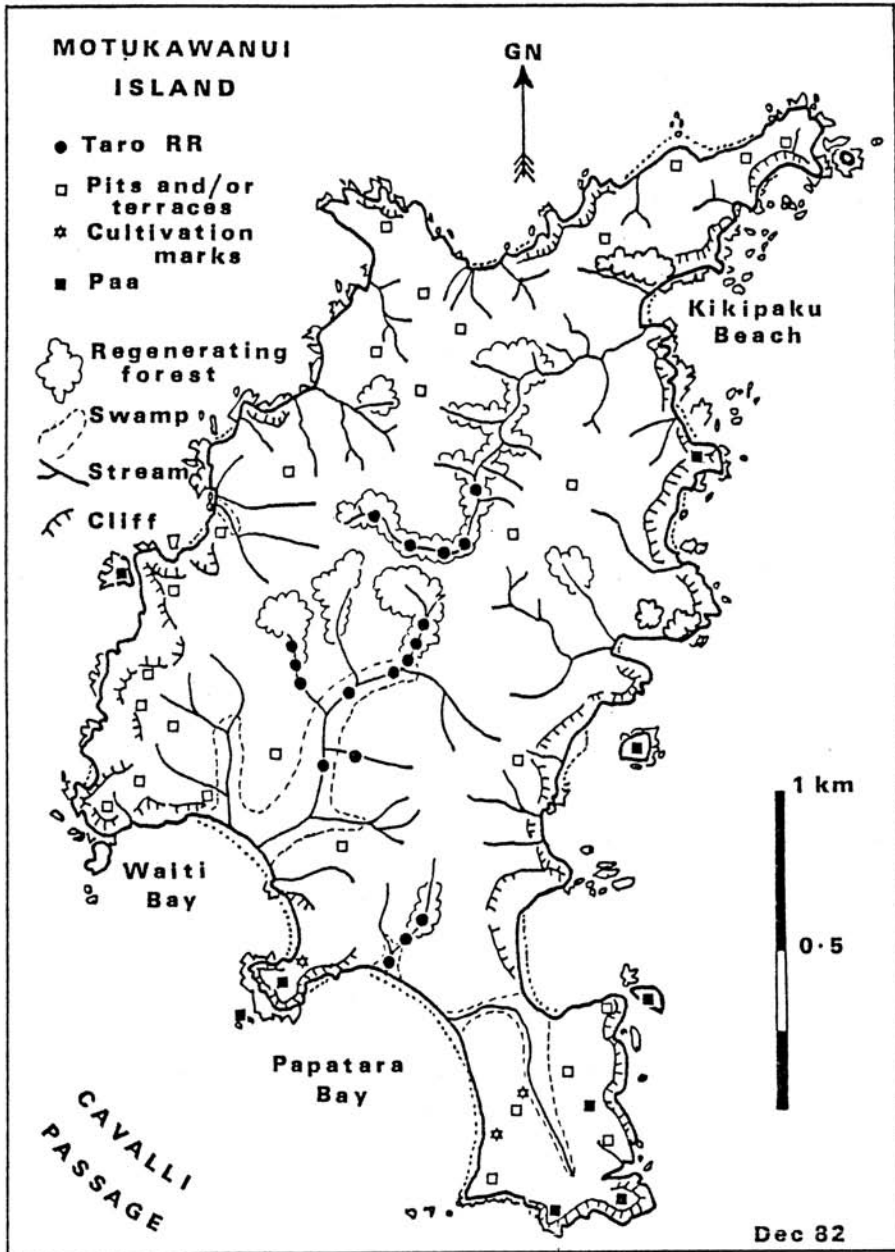


Figure 7.7 Distribution of taro (variant RR) and archaeological sites on Motukawauni, Cavalli Islands, Northland. Eight taro sites have been recorded although only five separate tributaries are populated. Map adapted from Hayward et al. 1979. See area map, Figure 7.3.

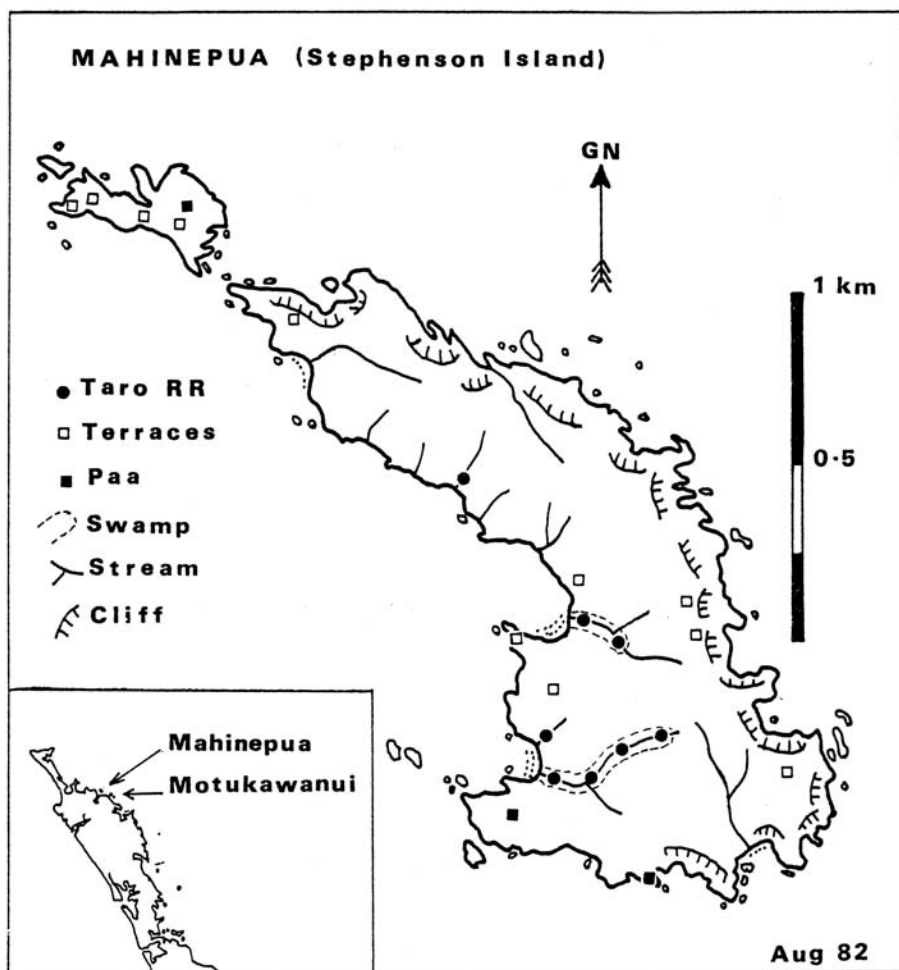


Figure 7.8 Distribution of taro (variant RR) and archaeological sites on Mahinepua, Northland. Four taro sites have been recorded, one for each populated water-course. Survey by A.E. Wright, Auckland Institute and Museum (pers. comm. 1982)

7.3.2 Cultural practices

The following observations were recorded while travelling through rural Māori communities. The records are extremely fragmentary since they were more or less incidental to the botanical survey rather than a serious attempt at full ethnographic description. The original field notes and a partially edited typescript of them are held by the Herbarium, Department of Botany, University of Auckland.

Unless specifically stated otherwise, the observations are best taken as applying to the variant RR, which predominates in both gardens and in the wild, and to which informants directly referred in many instances.

Use

The use of leaves (blades) was infrequently mentioned. Younger leaves are preferred for eating, but one informant said that leaves could be deribbed (central and side-veins of blade removed) to get rid of poisons. Contrary to the general opinion that variant GP is inedible, even after cooking, one informant said it is good but needs longer cooking. Recent influences on cultural practices were indicated when two Māori informants gave Pacific Island methods of cooking leaves, involving canned coconut milk, and when informants recalled, on perhaps two or three occasions, that Islanders had harvested leaves from local taro.

Another culinary use for leaves, mentioned only once, is for covering *hangi* (earth oven) stones to stop food burning on. Other uses are noted in the description of cultivation methods, below.

Use of petioles was never mentioned. Corms are the part generally eaten, after cooking by either boiling or roasting to remove poisons. One informant described splitting corms length-ways in half and letting them dry for half an hour in the sun until mucilage from the cut surfaces has dried off, prior to cooking and as a method for making them non-poisonous (the corms harvested by this informant come from a non-cultivated clump in a ditch by his house). Peeling the thick skin layer off corms is general practice prior to cooking.

Almost no information was gleaned regarding consumption of the variant GR. One informant whose plants came from a Māori cultivator some twenty years ago recollected that the 'small green' (variant GR) had been regarded then as sweeter and better than 'the red' (variant RR), although not as big. This statement may be presumed to refer to the quality of the corm.

Both the central corm and the larger side-corms from cultivated and non-cultivated plants were variously mentioned as the part consumed. Even the larger side-corms may be quite small (for example, approximately 5 x 3 cm, from a cultivated plant) but are recognised as best for eating by their dense or firm texture, pure and opaque white colour, and their non-coarseness. 'Coarseness' is a term which appears to describe more than just how fibrous corms are. Old corms or parts of corms which have become less dense, less opaque, and more fibrous, are described as 'coarse'. The small amount of food to be obtained from the smaller side-corms makes the effort of peeling them not worthwhile.

Feeding taro to pigs was frequently mentioned, particularly in Northland where variant GP was pointed out as inedible and good only for pigs. In one instance, poor, dry clay ground had resulted in corms of the variant RR that were unpleasant for eating ('fibrous and starchy') but which were cooked for pigs.

Many people mentioned *tangi* (funeral ceremonies) as occasions at which taro is served. One very old woman continued to cultivate taro in case (her daughter thought) it is requested as a food for a *tangi* at the *marae* (community meeting house) maintained by the family.

In the East Cape area, one particular locality, Torere (Figure 7.6), was remembered by many informants as the place where taro had been grown and served at *tangi*.

Although tangi were most frequently mentioned as occasions for use, taro also appears to be used for any large, temporary gathering requiring large amounts of food (for example, *hui* (community meetings), Christmas reunions, and when a large number of visitors stay at a marae). For some families with many rows of taro in their cultivations, use of the plant as a starchy staple may be of some economic importance. A number of informants and correspondents have said that there has been an upsurge of interest in cultivation and use of the plant, in recent years, or have expressed an increased interest themselves. Generally though, taro appears regarded with disfavour or disinterest, particularly by younger people. Older women with families recollect eating taro when they were children, and may now cultivate just one or two plants, or have non-cultivated clumps in their garden, to taste for themselves or to give to an older relative.

Cultivation

Of the areas surveyed, Northland was where cultivations or plantings of more than just one or two plants were most frequently encountered (Figures 7.1 and 7.2). Despite this, more recollections of past cultivation methods were recorded in the East Cape area. Taro is presently cultivated as a summer root crop, although in some cultivations clumps of more than one year in age had been allowed to form, possibly deliberately. In the Hokianga, informants regarded October as the time to plant and March the time to harvest, after the tops had died off. These dates are just a general rule. Late frosts have to be avoided in October; later plantings in November and December were reported. One informant gave March or April as harvesting times, and a harvesting in May was observed in the Bay of Islands. Southwards, in the East Cape area, planting is said to be in November, after the late frosts. M. Rau-Kupa (pers. comm. 1983) wrote from New Plymouth that planting is done when the weather is warm and frost-free, and harvesting is about March.

P. Tangiwai (pers. comm. 1983) wrote that leaves of two kinds of cultivated taro (*taro hoia* and *taro Tonga*) are harvested and eaten during the winter months.

Side-corms and the cut tops from corms were both mentioned as planting material or 'seed'. Planting material is initially obtainable from a wide range of sources: from locally known wild taro, from non-cultivated derelict or non-derelict gardens, and from the gardens of friends and relatives.

Once in cultivation, cut tops or smaller side-corms are obtained at the time of harvesting.

Planting itself was not observed, but methods currently used appear from reports to include or combine aspects of both traditional methods with methods common to kumara, potato, and other vegetable crops. One method of planting described, which appears to reflect tradition, is to place 'seed' (side-corms) in holes mulched with hay until the shoots appear (soil is presumably added for subsequent growth). During the hot summer weather, watering appears particularly important for taro.

M. Rau-Kupa (pers. comm. 1983) recommended cultivating taro in rich loam with compost. The larger taro cultivations of the Hokianga area were found in areas with rich alluvial loams.

For the over-wintering of planting material, a practice described twice in the field and once in correspondence is that of placing 'seed' on the ground outside with some sort of covering. Elaborations mentioned were placing the 'seed' on a matting of plant material, or in a shallow pit, and covering with taro leaves, or bracken fern and other plants, or sheet iron. The lattermost is valued for the warmth it gives the plants (M. Rau-Kupa pers. comm. 1983). This practice of sheltered but not dry storage indicates a need to maintain meristematic activity, during storage, as a guard against rotting. Another practice mentioned once is that of planting shoots during the winter and replanting them out in spring.

The statements of many informants about the original source of their plants indicated that the transfer of planting material about the North Island occurs over long distances between friends and relatives. Most reports described transfer within the three general areas surveyed, for example, between Kawakawa and Herekino Gorge (Northland, Figure 7.4), from one side of the Coromandel Peninsula to the other (Hauraki Gulf, Figure 7.5), and from Opotiki to Te Kaha, and Torere to Port Awanui (East Cape, Figure 7.6). Possibly the greatest distance reported was from Hamilton to Cape Runaway, East Cape (240km, straight line distance), from a daughter to a mother. At Motairehe, northern Great Barrier Island, an informant indicated that taro was quite possibly brought in from the eastern Bay of Islands (part of the same tribal district) during resettlement of the Island after World War I.

During the field surveys, it became apparent from the statements of informants that a major part of the transfer and cultivation of taro, as well as its cooking, is carried out by Māori women. However, the involvement of men was probably less fully recorded since most interviews were at houses and on weekdays, places and times at which encounters with men were less likely.

The fullest recollections of traditional cultivation were given by the Reverend Davis and his wife at Torere, East Cape, 19 January 1983. They described nearby taro gardens that existed some time ago (unspecified), on alluvial river soil by the river, and above the beach. There were several gardens, with fencing to keep stock out, and each garden had approximately twenty holes in which the taro were planted. The holes were scraped out using a piece of barrel-hoop iron which was also used to determine the spacing between each hole.

After digging the holes, sand was put over the whole patch and in the holes. The small side-shoots used as planting material were then placed on the sand in the holes. Clean, fine river gravel also was spread around the plants to the thickness of a hand. As the plants grew, the gravel was pushed up around them to attract moisture and keep the ground temperature up. Silty river gravel wasn't suitable because it gave weed problems, and beach gravel was too salty.

Plantings and later attentions were made at special times, and in wet weather like that 'at present' (19 January, a steady drizzle). The aim of cultivation and all the effort was to get just one large central corm.

As it grew the small side-corms were pulled off, 'like breaking off tomatoes', and older leaves and dry leaves were cut off and put on as a mulch, together with earth.

Shoots had to be sorted out and the leaves 'feeding' the desired corm preserved.

For storage after harvest, *tutu* (a common wild herb) was laid down as a mat and all the taro including 'seed' pieces were placed on this, followed by leaves from the taro plants.

The Reverend Davis also recalled that when young, he and his family lived in a village on the flat behind Okahau Bay, Auckland, where they also had gardens of maize, corn, kumara, and taro. This lasted up to the late 1930s, until they were ordered by the borough council to shift onto the hill.

The former gardens at Torere were mentioned or described by many people at other places around East Cape, as far as Port Awanui, just south of the Waiapu River. Torere is renowned both for these gardens and the serving of taro at tangi, while Te Kaha, nearby along the coast, is known for its kumara. Taro was not actually seen at Torere, but plants of variant RR at other sites were said to have come from Torere.

In the later descriptions it was further established that the gardens by the river at Torere had lasted up until twenty-five or thirty years ago (i.e. 1953–1958), and were communal gardens in an overall oblong area consisting of family plots, with boundary markers of round stones for each plot. An aerial photo taken in a 1948 mapping survey (Figure 7.9) shows what may have been among the last taro gardens in New Zealand cultivated by traditional methods. (It is possible that by 1948 the traditional methods were superceded even though taro cultivation continued).

The aspect of the traditional methods described by the Reverend Davis which seemed most often and clearly recalled by other informants, was that of mulching each plant individually by wrapping each successive, old outer leaf around the base of the plant, with or without first breaking off the leaf (informants varied on this point). Pushing gravel or soil up around the growing plant was also mentioned, though very rarely. The most common opinion of the old methods was that they had required a lot of care and effort. One very old man in the East Cape area recalled how potatoes had seemed a better proposition when he was young, while the old people then still had big patches of taro.

Non-cultivated sites

The occurrence of non-cultivated taro is frequently the result of neglect, either because a house and its associated garden have been abandoned (Figure 7.2, middle right), or because the taro has been discarded or has naturally escaped from a cultivated area and now propagates itself in an adjacent area of swampy ground, a stream, or a ditch (Figure 7.2, lower left).

It can be easily imagined that many wild sites have arisen by such a gradual transition of taro out of cultivations into natural watercourses, though this cannot be observed in a short-term study such as this. The statements of informants show, however, that plants may be moved by one of many routes between different types of site. A non-cultivated clump of taro may be planted and kept in a garden as an ornamental, as a reminder of the past and for an occasional taste, or as a potential source of planting material for future cultivation. One informant suggested that presently-wild taro had



Figure 7.9 The settlement Torere, East Cape, in September, 1948. Reconstructing from recorded oral history, the gardens visible by the upper arrow were probably used for taro cultivation over the following summer, and possibly for as many as ten more seasons. From these gardens taro were supplied for occasions at the nearby marae (lower arrow). Scale approximate only. Crown Copyright, Survey No. 371, Run No. 1753/6. New Zealand Aerial Mapping Ltd.

originally been planted in streams to preserve planting stocks, noting that they produce too much leaf and not a good 'root' (corm) in streams. Planting in the wild was reported by other informants also (Figure 7.2, upper right).

The harvesting of corms from non-cultivated sites can be at any time of year, though there are said to be times of year when the corms are less poisonous, a state which can be recognised by the amount of mucilage expressed at the surface of a cut corm (whether by more, or by less, was unfortunately not learned).

A number of informants lamented the fact that people had recently been digging up local non-cultivated patches (either in derelict gardens or wild) without replanting. Despite this problem, it appears generally acceptable in rural communities for anyone to use such sites when access is readily made from the road, or if permission is sought, and assuming care is taken to replant unwanted side-corms or cut tops. In a few sites the smoothly-cut ends of petioles were discovered, indicating recent harvests of the inner tender leaves. Although these observations were made in both summer and winter months, it seems likely that most harvesting of leaves occurs during the burst of leaf production over the warmer months.

Chapter Eight

Historical Implications and Future Research

This chapter has three main parts: (1) discussion of the present evidence, (2) a statement of the main conclusions, and (3) consideration of broader historical implications and future research on crop genetic resources and *Colocasia*.

8.1 Present Evidence

8.1.1 General distribution

The general geographic distribution of each variant provides, in itself, little evidence regarding history. The variant GR, for example, with a distribution apparently centred in Northland (Figure 7.4) could be a relic from the distant past, or it could have been of such recent origin that only limited dispersal has taken place. It is apparent that almost any explanation can be proposed for any geographic distribution in the absence of other kinds of evidence.

8.1.2 Site categories and plant transferral

The classification of New Zealand taro sites into cultivated and a range of non-cultivated categories, though necessarily loose, was made in the hope that some degree of historical perspective could be added to the observed distributions of each variant. An initial reaction to these categories is to suggest that they represent different points on a simple, linear historical sequence: cultivated sites becoming non-cultivated through neglect, then derelict, and finally the taro appearing in a wild setting.

Though such a sequence or route has undoubtedly often been followed, the cultural practices described above make it obvious that many alternative routes can lead to the creation of a taro site. Even with a good description of present day practices, speculating by analogy on the relative importance of different routes in the past would be hazardous. The present observations of geographic distribution, of occurrence in different types of site, and of cultural practices, therefore allow only two general, definite suggestions regarding history:

(1) the general history of each variant is different, since each variant can be distinguished by the combination of its general geographic distribution and its occurrence in different types of sites: variant RR is the most common overall (75% of identified taro), is common to all areas, and is found most commonly in non-derelict, non-cultivated gardens and in the wild; variant GR is less common overall (13% of identified taro), is most common in Northland, and is found most commonly in non-derelict, non-cultivated gardens; and variant GP is also less common overall (12% of identified taro), is also

most common in Northland, but is most commonly found in the wild (Figures 7.4, 7.5, 7.6, and Table 7.1).

(2) the transfer and planting of taro by people have been important mechanisms for its dispersal over long distances and into both cultivated and non-cultivated sites.

8.1.3 Site density and survey method

The highest density of sites appears to be in North Auckland and is the outcome of the interactions between land and climate, people, and the plant. The absolute frequency of taro per square kilometre in North Auckland may be high because of both a warm climate suited to its natural survival and because the same area attracts a greater density of people than other areas. The factors involved are complex and interdependent, and further discussion would require detailed geographic and demographic data from which quantities such as the per capita frequency of taro could be calculated. Such a detailed analysis could not be sustained with the present information which has been obtained in a rapid botanical survey.

Although the rapid survey methods used to find taro were undoubtedly biased in favour of sites near roads and around settlements, the use of these methods was justified by the practical limitations on time and finance. These limitations arose directly from the belief that a wide geographic coverage would give a less biased and more general view of the New Zealand taro population than detailed surveys of a few small areas or localities.

8.1.4 Archaeological sites

Exceptions to the rule of rapid survey were made for the surveys of Motukawanui, in the Cavalli Islands, and on northern Great Barrier Island. Rattenbury (1956) suggested that taro from the Cavalli Islands may have survived there 'since earliest known settlement', while Yen and Wheeler (1968) noted that specimens from Great Barrier Island and from Spirits Bay 'cannot be ascribed confidently to transfer in European times'. Following these suggestions and the report of taro sites on Motukawanui by Hayward et al. (1979), opportunities were taken to visit the islands in hope that detailed surveys would establish whether or not their taro can be regarded as 'archaeological'.

Samples of taro have been obtained from Spirits Bay, but a detailed survey was not made there. The settlement at Kapowairua, at the eastern end of Spirits Bay, was occupied earlier this century according to former residents now living at Te Hapua, nearby (O. Sutherland, DSIR, pers. comm. 1982), so it is quite possible that recent introductions have been made to the area. Taro often has been recorded in the New Zealand Archaeological Association site recording scheme as comprising all or part of an archaeological site. Archaeological sites are legally defined as more than one hundred years old (*Historic Places Act 1980*) but it is generally impossible to establish such antiquity for taro sites, since recent or present settlement is also commonly found associated with the archaeological landscape of paa, pits, terraces, and middens. This problem is particularly apparent along the western coast of Coromandel Peninsula (Figure 7.5) where wild taro is found at the entrances to a number of coastal gullies in possible

association with archaeological sites, but also only a few metres from the coastal road. The plantings could pre-date the road, they might represent plantings on a number of occasions distant or recent in time, or one person on one day may have driven along the road planting taro in gullies.

Motukawanui is the largest member of the Cavalli Islands (Figures 7.4 and 7.7), which were home to numerous Māori from pre-European times up to about 1900, with the first European encounter being made by Captain Cook in 1769 (Hayward 1979). Cruise (1824) recorded Cavalli Islanders offering vegetables for sale to his ship the *Dromedary* in 1820, and photographs at the Auckland Institute and Museum Library (Hayward et al. 1979) show in about 1900 a small village of Māori-owned huts behind the southern part of Papatara Bay. The island was farmed from the latter part of the nineteenth century up until 1974, and a homestead at the northern end of Papatara Bay was last permanently occupied about 1953 (Hayward 1979). Since 1978 the island has been part of the Bay of Islands Maritime and Historic Park.

On Motukawanui, taro (variant RR) was found in five tributaries and may therefore represent five separate plantings. Archaeological pit and/or terrace sites are distributed along the ridges, and the distribution of taro high in tributaries among remnant patches of native bush (Figure 7.1) suggests an association with past Māori occupation of the archaeological landscape. This occupation may have continued for some time after the encounter by Cruise in 1820.

The history of occupation of Mahinepua (Figure 7.7) is not known, though it has been farmed until recently without occupation, and is largely vegetated with ungrazed grass (A. Wright pers. comm. 1982). The distribution of taro (variant RR) here in four separate streams is suggestive of an association with past occupation of the archaeological landscape. Even without recent occupation, however, it is possible that plantings were made on both Motukawanui and Mahinepua in recent times by the Māori living nearby, on the mainland, and visiting the islands for various purposes (D. Simmons, Auckland Institute and Museum, pers. comm. 1983).

On Great Barrier Island, taro was not found in the unsettled, forested areas of the islands' northern end, despite an intensive search and the presence of a rich archaeological landscape. Although taro (variant RR) was found in settled areas nearby (Figure 7.5), this may be of recent post-World War I introduction from the eastern Bay of Islands according to a Māori informant at Motairehe, northern Great Barrier Island. Taro was present on the island in earlier times, since Kirk (1868) recorded it (as *C. antiquorum*) in a species list for the island. The present absence of wild taro in an unfarmed and presently unsettled part of the island is possibly due to the dense populations of pigs and goats inhabiting the native forest. Neither of these herbivores has been mentioned as past inhabitants of Motukawanui, where taro survives, although other islands in the Cavalli group have had pigs or goats (Hayward 1979). The survival of taro in the wild may require protection from dense populations of these herbivores, while pasture-fed stock probably pose little threat.

8.1.5 Cultural practices

Further interpretation of the distributions of the taro variants, beyond the two suggestions already enumerated, becomes speculative and involves further consideration of the cultural practices.

(1) Variant RR: This is clearly the most important variant as a food crop, and its dominance in both cultivated and non-cultivated sites does suggest that it has been more important in the past than the other variants, whatever the routes of plants into these sites. The range of sites indicated in the above statement is important — occurrence of the numerically dominant variant only in cultivations would strongly suggest something different, namely, recent adoption of a very popular cultivar.

(2) Variant GR: Speculation regarding variant GR is more difficult since almost no information about its cultural importance was obtained. This lack of information might not simply be due to a small chance of encountering both informants and the plant at the same time, since variant GP, with a similar low overall frequency, was quite often spoken about. It is quite possible that there is no common awareness of variant GR as a distinct type, since it is almost identical to variant RR in leaf shape and corm morphology (Chapter Five). The distinctive petiole colours of these variants may be generally ignored if, perhaps, there is little or no difference in the cooking and eating qualities of the two variants.

This discussion however does not lead to any favoured suggestion regarding history. Variant GR could be of old origin or introduction but may have been only slowly dispersed for some (not obvious) reason. Alternatively, variant GR could be young historically, without having had time to become widely dispersed. Factors affecting the rate and extent of dispersal may have included: (1) the close morphological resemblance to variant RR (Chapter Five); (2) arrival at a time after the introduction of European crops, when interest in trying a new taro cultivar may have been low; (3) a poor food quality not noted with the present limited observations; and (4) local cultural barriers to its dispersal from the point of origin or introduction. The restricted distribution of variant GR could be a relic of a formerly greater distribution if, for example, variant RR had been a more recent and popular introduction that displaced variant GR from cultivation, and if variant GR is incapable of surviving outside gardens (since it is mostly found in gardens). However, the one report of eating quality suggests that variant GR may be better than variant RR, and observations of the growth of variant GR (Chapter Five) give no indication that it is incapable of surviving without human intervention.

Historically, therefore, it seems likely that variant GR has always had a distribution limited to Northland since its appearance there. Whether this appearance was before or after the arrival of Europeans is not known.

c. Variant GP: The general absence of variant GP from garden sites undoubtedly reflects its poor eating qualities. Another reason for exclusion from gardens is suggested by the observation that stolon-producing taro, such as variant GP, are unpopular as cultivars in areas outside New Zealand because they require laborious repeated removal of the stolons to promote the growth of the central corm (Wilson 1982). A similar observation was made by Whitney et al. (1939), who noted that the two rhizome-

producing taro varieties in Hawai'i are commercially the least important of all the taros because the rhizomes increase the difficulty of cultivation and harvesting. It is more difficult to explain why variant GP has become dispersed in numerous wild sites. Two suggestions can be made which are not mutually exclusive: (1) that variant GP has been planted outside garden areas as a cheap source of pig food; and (2) that since its introduction the curiosity of people in a potential new food source has been sufficient reason for them to plant it in handy waterways, where no further care is required for it. They might also try it in gardens, but then soon discard it when the taste and growth habit prove undesirable.

The present general absence of variant GP from gardens makes it seem unlikely that its present distribution is relict from a formerly wider geographic distribution resulting from dispersal by people among gardens. Further, the good ability of variant GP to survive in the wild (Chapter Five) makes it seem unlikely that its present distribution is relict from a formerly wider distribution in the wild.

Variant GP may have become dispersed during the early nineteenth century as a food source for pigs, since pigs were raised by the Māori as an item of trade with the early European settlers (Hargreaves 1959).

Even if pig rearing was the main reason for the dispersal of this variant, the original introduction could have preceded the arrival of pigs. There is some suggestion from historical records that the variant GP was introduced by an early American whaling ship (Appendix 9), but no conclusive evidence exists regarding when this variant was introduced.

8.1.6 Site categories: analogy from the present to the past.

The different categories of taro site have been defined here partly on the basis of their present relationship to settlement of European design, to help distinguish between 'garden' and 'wild' sites. The attempt at a direct classification of historical status using such evidence (Matthews 1982) was not made here. It seems quite likely that a similar range of site categories existed in pre-European times in relation to Māori settlement. The relative importance of the different kinds of site would have been quite different though, since the cultivation of taro before the arrival of European crops was undoubtedly of much greater importance than afterwards. Non-cultivated taro in a variety of settings, garden or wild, could have had similar uses in the past as less labour-demanding, less controlled sources of food, and as sources of planting material.

8.1.7 The definition of cultivation

The observations of cultural practices make it apparent that cultivation is not the only way in which people aid the survival of taro in New Zealand. Deliberate dispersal of taro into non-cultivated sites is also important, though not the only means by which it may arrive in such sites. The replanting associated with the harvesting of taro from non-cultivated sites may well be necessary to the plant's perpetuation in the more frequently harvested sites (Figure 7.2, middle left, for example).

It is with the practice of replanting that the distinction between cultivated and

non-cultivated sites becomes unclear, since planting to some extent alters the immediate environment of the plants. As Zeven and de Wet (1982) note, people maintain cultivated plants in an artificial habitat if the plants are of sufficient value, while cultivation includes all kinds of agricultural practices, from merely protecting individual plants to actual planting or sowing, and tending of planted populations. The definition of a cultivated site used in the present study has been deliberately restricted to sites in which the soil appears cultivated, since consistent observation of the cultural practices attendant to the plants, over time, was not possible for every site. Even this restricted definition fails when the effects of people on the soil are indiscernable, though possibly important to the plants.

8.1.8 Traditional cultivation methods

Traditional cultivation methods similar to those recorded here were reported by Best (1976), who visited the Waiapu district near East Cape sometime before 1925, although in one respect the accounts differ. Best (1976) wrote that, in at least some cases, the innermost immature leaves were pinched off with the effect, reputedly, of increasing the size of the edible part. This seems an unlikely practice if the aim of cultivation was to produce a large central corm, as reported here for Torere. The expected effect of retarding apical growth in plants is to stimulate lateral growth (meaning, in the case of taro, the growth of side-corms). It is quite possible that this was the aim of cultivators in Waiapu district.

Since the cultivations at Torere appear to have been closely associated with the production of food for tangi, it is possible that especially large corms were desirable for public presentation. Methods for stimulating the growth of central corms may have been appropriate for publicly presented food, at special occasions, while the cultivation of side-corms may have been appropriate to mundane food production for ordinary consumption.

These suggestions need substantiation by people with traditional knowledge, and by further study of ethnographic records.

8.2 Main Conclusions

8.2.1 A taro variant of pre-European introduction?

The wide search for taro revealed only three taro variants of major geographic distribution. The distribution patterns of the variants RR, GR, and GP differ, but are not readily interpreted regarding two questions of history:

- (1) Which, if any, of the three variants are of pre-European origin or introduction?
- (2) Have pre-European distribution patterns of taro been perpetuated to the present, or have they been totally obscured by recent dispersal and loss?

Since the distributions of these three variants together span a wide geographic range in which other taro appear almost completely absent, perhaps one of them – at least – is of pre-European origin. Variant RR is predominant numerically, in the range of settings it occupies (including possibly archaeological sites), and in cultural importance. It therefore

seems the most likely taro variant to have been introduced in pre-European times (if any of them were so introduced).

This argument requires two suppositions; namely that taro was introduced in pre-European times (as indicated by first-eyewitness European records, and Māori tradition), and that not all pre-European taro was lost from cultivation, or was unable to survive without cultivation, after recent introduction of the taro varieties found now.

If the first argument is correct and taro of pre-European introduction is still present, it seems unlikely that its pre-European distribution pattern has been totally obscured. To identify a particular distribution pattern as pre-European would, unfortunately, entail a circular argument. The suggestion that variant RR is the most likely taro to have been introduced in pre-European times is largely based on its present abundance, without assuming that its present distribution reflects a pre-European pattern.

8.2.2 A taro variant originating in New Zealand?

Whitney et al. (1939) described varieties of the group *Lauloa* previously reported (Hawai'i Agricultural Experiment Station 1937) to have arisen by vegetative mutation in the varietal collection. The new mutants resembled already established varieties (Hawai'i Agricultural Experiment Station 1937). The *Lauloa* varieties are all distinguished by differences in the colouration of various parts of the petiole. (Whitney et al. 1939).

These reports suggest another explanation for the distribution of variant GR: this variant may have only recently dispersed after origin as a colour mutant of variant RR (although another explanation, perhaps less likely, is that variant RR originated a long time ago as a colour mutant of variant GR). This is consistent with the observations of similar leaf shape and corm morphology (Chapter Five) and similar karyotypes (Chapter Six) for variants RR and GR. However, the suggestions must remain tentative pending definitive cytological observations and investigation of the basis for the colour difference (green versus red) in the petioles.¹⁾

8.3 Wider Implications

8.3.1 Historical interpretations

Three taro variants with a chromosome number of $2n = 42$ appear predominant in New Zealand today. The present field evidence and records of cultural practices provide circumstantial evidence that taro of $2n = 42$ could have persisted since pre-European times in two ways:

(1) Naturally. The taro observed readily grow and self propagate vegetatively without human intervention.

(2) With human intervention. Taro has probably never fully ceased to be planted and cultivated as a food crop since its introduction to New Zealand.

Accepting this suggestion of persistence $2n = 42$ taro since pre-European times could lead to the suggestion of a pre-European transfer from the southwestern Pacific to Aotearoa, while the evidence from archaeology, physical anthropology, and language demonstrate Māori origins in the southeastern Pacific, in Polynesia (Bellwood 1978;

Davidson 1979). This interpretation is however not secure because it is just one of a wide range of possible explanations for the present predominance of taro with $2n = 42$, and the scarcity of taro with $2n = 28$:

(1) Plants with $2n = 42$ were introduced in pre-European times (and/or after European influx) from the southwestern Pacific, where this chromosome number has been recorded.

(2) Plants with $2n = 42$ were introduced — in pre-European times, and/or after European influx — from Polynesia, where extensive sampling may have yet failed to detect taro present with this chromosome number.

(3) Plants with $2n = 28$ were introduced in pre-European times, but failed to survive when the introduction of European crops and new cultivars of kumara led to the general neglect of taro.

(4) Plants of $2n = 28$ were introduced in pre-European times and still survive, but did not become dispersed in the areas searched during the surveys reported here.

(5) Plants with $2n = 28$ were never introduced in pre-European times, despite human colonisation from Polynesia.

(6) Plants of $2n = 28$ were introduced in pre-European times and gave rise to $2n = 42$ polyploids which somehow displaced the parental stocks.

These possible explanations and some implications for future studies are discussed next:

(1) and (2) Introduction of taro with $2n = 42$: An important aspect of the present observations is that taro of $2n = 42$ are not of uniform morphology or karyotype. Although chromosome numbers alone are suggestive of links between different regions of the Pacific, they are not sufficient to verify them. Presently, neither morphological nor genetic descriptions exist, which allow closer comparison of the New Zealand taro with taro of $2n = 42$ in the southwestern Pacific. The discovery of phenotypically and genetically close relatives of the New Zealand taro variants in overseas locations would indicate possible geographic origins and would allow more selective examination of historical records relevant to the issue of recent introductions (see Chapter 14).

It is difficult to judge how well the Polynesian region has been covered by sampling. Yen and Wheeler (1968) report counts of $2n = 28$ for 65 varieties from the Polynesian region outside New Zealand. Further varieties with chromosome counts of $2n = 28$ have been found in the area but have not appeared in published reports (D. Yen pers. comm. 1983). The number of varieties observed is on its own a poor basis to judge the quality of the data, since the spatial distribution of samples must in theory affect the chance of observing variation. Varieties sampled from one garden area would in general be less likely to exhibit variation than samples from a diverse range of natural and artificial habitats on one island. Yen and Wheeler (1968), in what was an exploratory study, used a Pacific-wide sampling approach with the aim of associating plants and people in theories of migration. Their descriptions of sample sources are minimal, but it is obvious that for such a general aim, the practical limitations imposed on the observation of local distributions are vastly greater than for the present study of taro within New Zealand.

According to the aims of these studies, Pacific-wide and within New Zealand (and

given the constraints of time and funding), compromises have been made between the ideals of wide sampling range and thorough sample description.

With the above considerations in mind, it appears that if a future study has the aim of identifying possible overseas origins of New Zealand taro then some effort will be justified for establishing the local distributions, and both natural and cultural associations, of taro found within the chromosome number $2n = 42$. This may be particularly important in the Polynesian region and other areas opened to modern shipping and road transport, because it is known that varieties held in the collections of agricultural field stations soon become dispersed amongst local cultivators (R. Fullerton, DSIR, pers. comm. 1982; D. Yen pers. comm. 1983).

The best initial strategy for future studies may be to look at existing, well-provenanced living-plant collections as well as in areas more or less isolated from recent wide-ranging transfer of taro cultivars. Long-established collections with material collected from what were, at the time, isolated locations may be an ideal starting point.

(3) Extinction of taro with $2n = 28$: The possibility that taro of $2n = 28$ are unable to survive in New Zealand without human intervention cannot be sensibly discussed until field trials are made with such taro in New Zealand, in a range of habitats.

(4) Insufficient sampling: Since two major variants are more or less restricted to Northland, it is quite possible that the variants with $2n = 28$ from New Plymouth have a wider and historically important distribution in the Taranaki area. A general field survey of the Taranaki area would be valuable if it established the extensive distribution (or otherwise) of such taro.

(5) Non-introduction of taro with $2n = 28$: Given the long-standing importance of aroid root-crops for Pacific horticulturalists (Bellwood 1980), it seems quite unlikely that taro of $2n = 28$ were never introduced from Polynesia in pre-European times. Nevertheless it should not be assumed that all voyagers brought taro with them.

(6) Diploids give rise to triploids in New Zealand: It is unlikely that polyploidisation and displacement led to the predominance of taro with $2n = 42$ chromosome numbers. The number $2n = 42$ cannot be derived from $2n = 28$ by a simple doubling of the somatic cell chromosome number in an apical meristem, in the absence of breeding and seed production.²⁾

The import of taro for a wide range of immigrant ethnic groups is significant for the present discussion. While it is estimated that 97% of present commercial imports are from Samoa and Tonga (J. Watson pers. comm. 1982), and are therefore probably of $2n = 28$ chromosome number, it is possible that taro has entered directly, or indirectly (Yen and Wheeler 1968), from Asian sources where the number $2n = 42$ is present. Any information about imports of vegetables for immigrants during the nineteenth century would be of interest.

8.3.2 The genetic evaluation of crop plants

In conclusion to a discussion of crop germplasm conservation and developing countries, Plucknett et al. (1983) state that 'currently, the phenotypic characters of accessions are noted rather than the genes of the plants; in the future, the usefulness of gene bank

records will depend on the relevant gene symbols being recorded for each accession'.

It is clear, however, that the evaluation of crop germplasm has generally been conducted on a sporadic basis depending on the particular interests of specialists in such fields as pathology, entomology, plant physiology, and agronomy. If gene banks are to be evaluated genetically prior to the investigations of such specialists, and in order to aid them, then the study of plant phylogeny is likely to be the most useful field of investigation, since it provides a general basis for understanding and predicting the occurrence of phenotypic attributes.

Within the study of phylogeny innumerable strategies may be adopted. Traditional taxonomic methods based on the analysis of morphology, and biochemical studies of protein phenotypes, may be used to identify genetic relationships indirectly. Both approaches suffer from developmental and environmental effects on gene expression and require verification using breeding and inheritance studies. Recent developments in molecular biology make it possible to directly identify and compare the nucleotide sequences of DNA. The occurrence of certain sequences of nucleotides also may in essence be phenotypic, since developmental and environmental effects on the replication and transcription of genes are now being revealed. Not all directly examinable aspects of genomes are suitable for phylogenetic analysis.

Given the large range of options available for studying phylogeny, particular aims must be made explicit to develop a rational strategy for the evaluation of crop plant gene pools.

The evolution and dispersal of crop plants is dependent in various ways upon their interaction with humans, so that the study of crop plant phylogeny is in effect a study also of human cultural history. A strategy of phylogenetic analysis aimed at clarifying the relationships between plants and humans must benefit the understanding of both.

During the present study, some consideration was given to developing a strategy for the genetic analysis of *C. esculenta*, and an initial attempt to characterise the leaf protein ribulose-1, 5-bisphosphate carboxylase-oxygenase (RuBP carboxylase) is described in Appendix 11.

The genetic basis of RuBP carboxylase is now particularly well understood, though by no means completely. The native protein consists of two kinds of subunit, a large one encoded by chloroplast genomes and a small one encoded by the nuclear genome. Genetic analyses of the modes of inheritance demonstrate maternal transmission of genes for the large subunit and biparental transmission of genes for the small subunit (Uchimiya et al. 1977; Miziorko and Lorimer 1983). The polypeptide banding patterns of the dissociated subunits (eight large and eight small subunits) after polyacrylamide gel electrophoresis and isoelectric focusing have been frequently used for studying plant phylogeny, although recent work has revealed a major methodological artefact (O'Connell and Brady 1981).

Studies of the polypeptide banding patterns of the large subunit reveal little variation within and between genera (for example, only four types within the entire genus *Nicotiana*, Uchimiya et al. 1977), while more variation is observed for the small subunit (Chen et al. 1976; Cammaerts and Jacobs 1981). Recent studies of chloroplast DNA

using restriction endonucleases have shown the nucleotide sequences of the large subunit genes of maize and spinach to be highly conserved with 84% homology, corresponding to an overall amino acid homology of about 90% due to silent nucleotide changes (Whitfield and Bottomley 1983). It is apparent that the small amount of genetic variation revealed by the large subunit of RuBP carboxylase severely limits its utility for phylogenetic analysis.

Gatenby and Cocking (1978) note, in conclusion to a study of RuBP carboxylase in *Solanum*, that the analysis of chloroplast DNA with restriction enzymes is a more sensitive method for identifying chloroplast genomes than analysis of the large subunit of RuBP carboxylase. Restriction endonuclease digestion of total chloroplast DNA has now been used to establish a phylogeny for species of *Lycopersicon* and *Solanum* (Palmer and Zamir 1982). Although an extremely limited amount of sequence divergence was observed among the DNAs, use of a moderate number (25) of different restriction endonucleases revealed sufficient variation to permit construction of a detailed chloroplast DNA phylogeny essentially free of ambiguity. Major sequence rearrangements are generally quite rare during chloroplast genome evolution, so changes in restriction fragment patterns can usually be interpreted as the consequence of base substitutions rather than DNA rearrangements (Palmer and Zamir 1982). The phylogeny obtained for mainly *Lycopersicon* and some closely related *Solanum* species is generally consistent with relationships based on morphology and crossability but provides more detailed resolution at several places (Palmer and Zamir 1982).

From the above studies it is apparent that a compromise must be made between two conflicting needs for the study of relationships between plants and people: (1) the need for the sampled part of the plant's genetic system to have been sufficiently variable to result in differentiation during the course of human history; and (2) the need for a sufficiently stable part of the plant's genetic system to allow a phylogeny to be established unambiguously.

Further, in order to relate phylogeny to geographic distribution and to dispersal by humans, consideration must be given to differences in the transmission of different components of the plant's genetic system. In theory, if natural geographic and genetic dispersal of a genetic component is limited, then the effects of dispersal by humans should be more clearly evident.

Chloroplast genomes appear to fit the criteria indicated above. They appear both genetically stable and sufficiently variable for their use in evaluating evolutionary relationships amongst plant species within a genus (Palmer and Zamir 1982).³⁾ In addition, the natural geographic dispersal of chloroplast genomes appears more limited than nuclear genomes because:

(1) Assuming strict maternal transmission, dispersal of chloroplast genomes depends on the dispersal of vegetative parts and seed. Pollen provides an additional mode of dispersal for nuclear genes. In some plants sexual reproduction may be rare or non-existent, so that dispersal of both plastid and nuclear genomes is either by relatively localised natural dispersal of vegetative parts, or by people who use vegetative parts for propagation.

(2) Assuming strict maternal transmission only, opportunity does not arise for a hybrid mixture of chloroplast populations within an individual plant, c.f. hybridisation and sexual recombination of nuclear genomes, and other mechanisms of molecular evolution in nuclear genomes.

In theory, these limitations on chloroplast dispersal will have resulted in more tightly defined boundaries of geographic distribution for variants of chloroplast genomes than for nuclear genomes. With plants in which mitochondria are also maternally transmitted, *Coffea* for example (Berthou et al. 1983), a similar argument may apply.

The primary purpose of this discussion has been to develop a strategy for the future study of *C. esculenta*. However, if the foremost aim in future is to clarify the cultural history of humans, the consideration of genetic transmission in plants may indicate more suitable genera for study. This will also depend of course on the plants present in the geographic region entered. To conclude the present discussion however, a number of questions are posed regarding the evolution of *Colocasia*:

(1) Where is the natural origin of this genus and to what extent have humans been responsible for its wide dispersal throughout the tropics and sub-tropics? The aroid genus *Xanthosoma* originates in South America, while *Colocasia* and other edible aroids are found in Asia and Australasia (Leon 1977). Does this indicate that the genus *Colocasia* may include endemic populations in the different continental areas, arising during the geological history of Gondwanaland?⁴⁾

(2) What has been the importance of sexual hybridisation in the evolution of cultivars and can the phylogeny of cultivars be related to the dispersal and mixing of cultivar populations by people?

(3) What combination of phenotypic and genetic characters is best observed to identify particular subspecies or cultivars, and to allow comparisons between them?

(4) Do plants that are phenotypically and genetically identical to the New Zealand variants of taro exist outside New Zealand, or has evolution obscured origins?⁵⁾

Notes

- 1) The ribosomal DNA (rDNA) patterns of var. RR and var. GR were subsequently found to be identical (see Chapter 14). They were also found to be similar to the rDNA patterns of certain Japanese and Chinese taro cultivars, lending support to the interpretation of historical introduction to New Zealand by Chinese immigrants in the 19th century.
- 2) Short, relatively cool summers and long cool winters in the North Island of New Zealand (latitude range approx. 34.5 – 45.5 degrees S) prevent fruit and seed development. In Okayama, Japan (approx. 34.5 degrees N), it has been possible to breed taro experimentally by using a hothouse to raise temperatures and extend the growing season (Yoshino pers. comm.; see Yoshino 2002). It may be possible to breed taro in the Far North of New Zealand, using hothouse conditions and artificial lighting to extend the growing period of taro.
- 3) The value of chloroplast DNA analysis has been recently confirmed for taro, through complete sequencing of the chloroplast genomes of var. RR and var. GP, and testing of a wide range of taro samples; see Ahmed et al. (2012, 2013).

- 4) There is currently no evidence that the natural range of genus *Colocasia* extends beyond the continental regions of Sunda and Sanul. The evolutionary diversification of Family Araceae is discussed in relation to Gondwanaland and continental drift by Nauheimer et al. (2012).
- 5) Plants that are phenotypically and genetically *similar* to the New Zealand triploid cultivars have since been found outside New Zealand (see Chapter 14); full-genome sequencing is now technically possible and could be used to confirm clonal identity with complete certainty. The term ‘evolution’ is more usually used in relation to long-term processes of genetic and phenotypic change; in the present context, it is better to consider the possibility that cultivar origins have been obscured by processes of selection, domestication, dispersal, and cultivar replacement over periods of thousands or hundreds of years (and possibly over periods of decades, given the speed with which devastating plant diseases can spread; see Chapter 17 comments on *Phytophthora colocasiae*).

PART 3

THE ORIGINS, DISPERSAL, AND DOMESTICATION OF TARO

In the preceding chapters (Part 2), I reported the survey and analysis of taro in New Zealand, a country located far from the likely geographical origins of the plant in Southeast Asia. Where exactly did the taro varieties growing in New Zealand and the Pacific Islands come from? To approach this question it was necessary to look westward to Australia, Papua New Guinea, and beyond into Asia. In Chapters Nine to Sixteen (Part 3), I describe the full geographical extent of wild taro in Australia for the first time. Analyses of ribosomal DNA variation were made after preparing recombinant plasmids with fragments of nuclear rDNA extracted from taro. In a survey of taro from Australia, Papua New Guinea, Asia, and the Pacific Islands, wide-ranging size variation was discovered among rDNA spacer fragments, in addition to the geographically widespread occurrence of what may be a single rDNA variant, in both diploid and triploid taro, from wild and cultivated habitats.

Investigations of chloroplast and mitochondrial DNA, and nuclear rDNA, and comparisons with other Colocasioid taxa, confirmed the taxonomic integrity of *C. esculenta*, consistent with suggestions for a single geographical origin of the species within mainland Asia. Restriction site mapping of the cloned rDNA fragments from taro, and *in situ* hybridisation to chromosomes, demonstrated that taro rDNA is structurally similar to rDNA in other eukaryote taxa. Ribosomal DNA variation in taro was therefore interpreted, in part, by analogy to other taxa. Variation in taro rDNA was also interpreted in terms of possible local and long-distance dispersal by humans and natural vectors, within and between Asia and the Pacific.

The possibly natural origins of wild taro in Australia and New Guinea are discussed and then related to a broader view of origins, dispersal, and domestication of the species. Part 3 is adapted from Matthews (1990).

Chapter Nine Taro in Prehistory

9.1 Vegeculture and the Origins of Agriculture in New Guinea

Colocasia esculenta (L.) Schott, commonly known as taro, belongs to the pan-tropical and monocotyledonous family Araceae. In prehistory, before the modern era of world exploration, the cultivation of taro extended to Japan and southern China in the North, New Zealand in the South, Africa and southern Europe in the West, and Polynesia in the East (Leon 1977; Petterson 1977; Cable 1984). Within these extremes taro was, and still is, associated with diverse forms of agriculture, from forest swiddens to permanent fields, in drylands and wetlands (deYoung 1960; Peralta 1982; Spriggs 1984; Thaman 1984). The introduction of taro to the Americas is attributed to European shipping from Asia during the nineteenth century (Plucknett 1976). Taro is one of many crops introduced to Africa from Southeast Asia in prehistory (Purseglove 1976). Production of taro by traditional methods has declined with the recent worldwide decline of subsistence agriculture and its replacement with cash-cropping (Wang 1983). Taro has not become a major cash crop, and on a broad scale the present geographical distribution of cultivated taro reflects mostly prehistoric processes, unaffected by very recent dispersal.

Wide debate exists regarding the relative antiquity of agricultural systems that depend mainly on the reproduction of crops by vegetative reproduction (vegeculture) and those that depend mainly on plants propagated by seed (seed-culture). This debate, reviewed by Harris (1972), has various expressions according to the different suites of crop species found in Africa, Southeast Asia, and South America. In tropical Southeast Asia, taro and yams (*Dioscorea* spp.) are the major vegetative staples, and rice (*Oryza sativa*) is the major seed staple.

Since the 1940s, a number of botanists and geographers have suggested for Southeast Asia that seed-culture dominated by rice replaced an older vegecultural system, characterised by a suite of root crops, fruit trees, and nut trees, still thriving in New Guinea and the South Pacific islands (Harris 1972; Spriggs 1982; Golson 1985). This view was questioned by Gorman (1977), who suggested that rice and taro were domesticated at the same time from wild progenitors in swampy habitats in mainland Southeast Asia.

The aspect of prehistory of central concern here is the relationship between taro and human settlement of Sahul, the continental plate to which New Guinea and Australia belong. Among the traditional food plants of the Australians and the New Guineans are a number of genera and species familiar as cultivated starch sources in Asia and Oceania (Golson 1971a; Yen 1985a, 1985b). These include *Musa* spp. (bananas), *Dioscorea* spp.

(yams), *Ipomoea* spp., and taro. In Australia, wild taro are utilised, according to ethnographic records, within a hunting and gathering context (Roth 1901; Levitt 1981; Crawford 1982; Jones and Meehan 1989). In New Guinea (Irian Jaya and Papua New Guinea) taro also are wild, but are best known ethnographically as cultivars within wetland and dryland agricultural systems.

Human settlement of the continent Sahul occurred by 40,000 years ago, in the late Pleistocene (Jones 1988; Allen 1989). Archaeological and other evidence from Kuk, a swamp site in the Western Highlands of Papua New Guinea, indicate a sequence of agricultural practices from a claimed date of 9000 years ago (Golson and Hughes 1980; Gorecki 1986; Golson 1989). Although no remains of recognisably cultivated plants were recovered from the earliest deposits, the present wild and cultivated flora of New Guinea and nearby islands provide many candidates for early cultivation.

Yen (1971, 1973, 1982, and 1990 in preparation) has developed the hypothesis that agriculture in New Guinea had an early and independent origin and elaboration, based on the domestication of a range of Melanesian plants that included basic staples, vegetables, and fruits able to sustain populations in various environments. With the subsequent arrival of colonists from Asia came the introduction of a number of already domesticated plants, including taro, various yam species, and the *Eumusa* section of bananas. The position of taro in this hypothetical sequence was noted by Yen (1982) as being equivocal. Although it has been generally accepted, on linguistic grounds, that taro entered the Pacific relatively recently (c. 4000 years BP) with Austronesian speakers of Asian descent (Pawley and Green 1973; Blust 1988), suitability for wet conditions made taro a candidate for earlier cultivation at Kuk swamp (Golson 1977). If direct palaeobotanical evidence is found for cultivation of taro at such an early date, this could reflect the introduction of cultivated taro before Austronesian speakers arrived, and/or the selection and domestication of taro already present in the pre-agricultural flora of New Guinea. Yen (1982) suggested that so-called feral taro in New Guinea and Northern Australia could in fact belong to the natural eastward extension of the Indo-Malaysian flora. The challenge here for botanical research is to determine whether or not taro contributed to an indigenous development of agriculture in New Guinea, and to assess the likely agricultural connections with Asia suggested by the presence of Austronesian speakers in coastal Melanesia and Oceania.

9.2 Early Botanical Observations

In what remains the most thorough general taxonomic treatment of the genus *Colocasia*, Engler and Krause (1920) described the home of *C. antiquorum* (synonym for *C. esculenta*) as being doubtless in island Southeast Asia ('Ostindien'). They noted, however, that the species frequently becomes wild along stream banks, assuming the appearance of a natural part of the flora in tropical and subtropical regions. In June 1770, the botanist Joseph Banks made a detailed description of taro at the Endeavour River, Northeast Queensland (Banks 1770, see Appendix 12), and collected taro in Australia that year (Figure 9.1), probably also at the Endeavour River. These records, made before

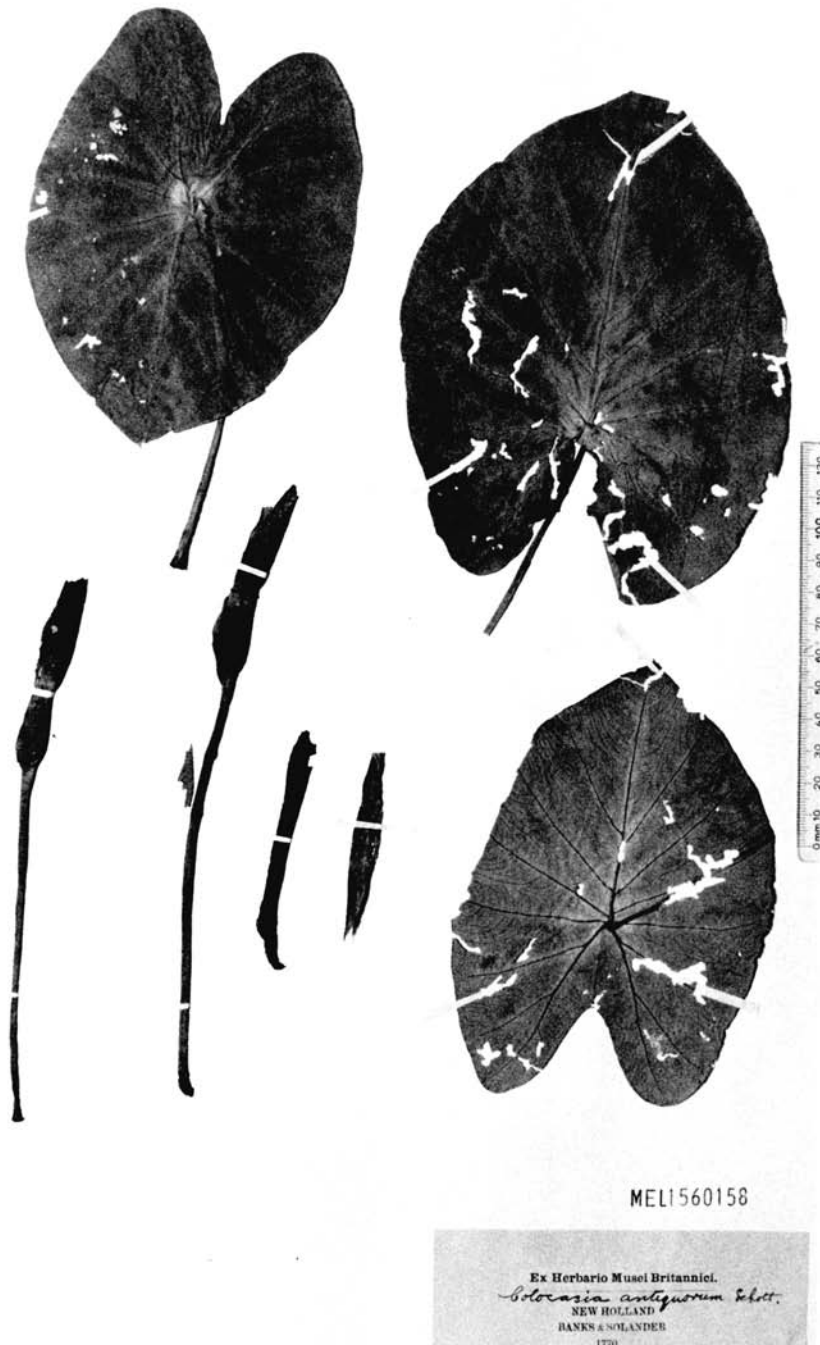


Figure 9.1 Australian specimens of *C. esculenta* collected by Joseph Banks in 1770. Note inflorescences on long peduncles, lower left. From the Melbourne Herbarium (an Australian specimen, collected by Banks in 1770, is also located at the Natural History Museum of Paris).

colonisation by Europeans, prove that taro was present in Australia in prehistory. The naming of taro within traditional Aboriginal classification systems also points to its antiquity in Australia (Jones and Meehan 1989: 127).

Ferdinand von Mueller (1865–1866), botanist at the Royal Botanic Gardens, Melbourne, described taro as ‘apparently also indigenous in the warmer parts of East Australia’, and Cheeseman (1900) reported taro as ‘truly native in India and Malaya, and possibly also in some Pacific Islands’. Spier (1951) summarized previous observations as follows:

Examination of the botanical literature reveals that little attention has been paid to the ultimate origins of many widespread plants. Taro (*Colocasia*) is, unfortunately, one of those so neglected. Even the great historical botanist, de Candolle, is vague about its origins, placing them in India, Polynesia, and the Malay Archipelago (de Candolle 1884). It seems probable, from other evidence, that we can rule out the last two of these, or at least Polynesia. Dispersion of the plant into Polynesia apparently followed human occupation of the region. This question hinges on the distribution of wild varieties of *Colocasia*. Burkill, in mentioning the presence of the wild plant in Polynesia, says that this is due to its robustness, not to its being a true native (Burkill 1935). Apparently here the “wild” form is not truly wild but escaped from cultivation. However, in continental Asia the case may well be somewhat different. Watt (1889), Balfour (1885), and Burkill (1935) all make references to wild varieties in tropical India: these are references to varieties of *C. antiquorum* and *C. esculentum*. In addition Watt states that *C. antiquorum* is found wild in Ceylon, Sumatra, and several islands of the Malay Archipelago I should be inclined to agree with Burkill’s analysis of the situation and his statement that *Colocasia* is a native of India and elsewhere in Southeast Asia.

9.3 The Origins and Natural Geographical Range of Taro

In addressing the question of geographical origin, previous writers have not been explicit about whether they are referring to the origins of taro as a natural species, or to the origins of cultivated taro. If it is assumed that *C. esculenta* originated somewhere as a natural species, before humans were present, and that the geographical range was not extended by humans, then it follows that the origins of cultivated taro were within the natural geographical range.

Previous authors attempting to identify natural geographical range through observations of wild taro could not distinguish between plants ultimately derived from introductions, and of natural occurrence (early authors cited by Spier 1951, above; Hotta 1983; Matthews 1987, for example). The difficulty in identifying naturally occurring plants in the wild is compounded by the possibility that non-agricultural societies altered the distributions of the plant species they utilised (Ford 1985; Rindos 1984; Chase 1989; Yen 1989). Wild taro could have been introduced to wild habitats in areas beyond the natural geographical range of the species, before any association with agriculture. Contrary to the initial argument above, cultivated taro might not have originated within

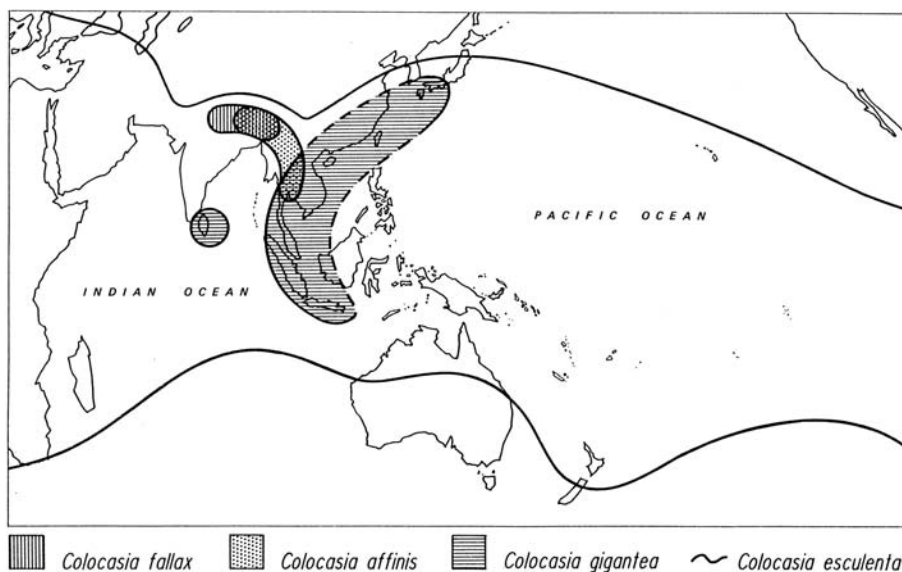


Figure 9.2 Distribution of *C. esculenta* (Africa to Americas), and other *Colocasia* species in Asia. Dotted lines indicate where the boundaries for *C. gigantea* are considered uncertain. See Appendix 13 for details of records.

the natural range of the species.

Practical and objective criteria for distinguishing indigenous and introduced taro are not obvious. In this thesis I describe progress towards establishing such criteria. Defining the natural geographical range of taro will be a major advance for investigating the origins of cultivated taro, and the origins of agricultural systems that were possibly based on taro cultivation.

9.4 The Origins of Taro as a Natural Species

Engler and Krause (1920) described seven species of *Colocasia*, but only four of them have been collected more than once, as revealed in a search of European herbaria in 1984 and 1985. These were *C. fallax* Schott; *C. affinis* Schott; *C. indica* (Lour.) Hassk., synonymous with *C. gigantea* Hook. f. (Hotta 1970); and *C. antiquorum* Schott, synonymous with *C. esculenta* (Linn.) Schott (Hill 1939). Figure 9.2 shows the distributions of these species based on herbarium records and published floristic accounts (Appendix 13). Records for the poorly known species, *C. gracilis* from Sumatra, *C. manii* from Assam, and *C. virosa* from Bengal, are given in Appendix 14. Because all the other species of *Colocasia* are confined to Northeast India and Southeast Asia, it is proposed here that *C. esculenta* originated in this area. If phylogenetic relationships between the four species are determined, it will be possible to locate the origin of *C. esculenta* more closely within Southeast Asia, depending on which of the other species is

most closely related. For this reason, investigations with species of *Colocasia* other than *C. esculenta* were initiated and are described in this thesis.

The species *C. fallax*, *C. affinis*, and *C. gigantea* have much smaller geographical ranges than *C. esculenta*. *C. gigantea* is more widely distributed than the other minor species, which probably reflects its status as a lesser food crop of Southeast Asia. In southern Japan, *C. gigantea* is cultivated as a leaf vegetable (Hotta 1970), and the leaves are also eaten in Sri Lanka (V. Amarasinghe, pers. comm. 1985). Heyne (1927: 425; cited by Burkill 1966) reports that the fruit is used as a flavouring, and Li (1979) notes medicinal uses of *C. gigantea* stems. Although *C. gigantea* commonly bears fruit with many fully formed seeds (unpublished herbarium records) and might be easily dispersed by natural means, it is likely that humans have dispersed *C. gigantea* beyond its natural geographical range to some extent. The restricted ranges of *C. fallax* and *C. affinis* today are probably close to what are the natural ranges, since these species are little utilised. Li (1979) notes that *C. fallax* is used as a leaf vegetable in Yunnan, southern China, where the species is found in dense valley forest and shrublands, and *C. affinis* var. *jenningsii* is a rare ornamental in horticultural contexts outside Asia (personal observation). Dispersal of ornamental forms of *C. affinis* could have extended the geographical range of this species within Asia. No other records of the utilisation of *C. fallax* and *C. affinis* are known to the present author. Utilisation of *C. esculenta* as a food is commonly reported and all parts of the plant (corm, leaf, and inflorescence) can be eaten. Medicinal utilisation of taro is also common.

The above observations show that species of *Colocasia* other than taro are either not cultivated or are cultivated to only a minor extent, and assuming that this was the pattern in the distant past, then it is unlikely that *C. esculenta* first evolved within cultivation from one or more of the other species. Rather, it is proposed here that *C. esculenta* evolved as a natural species in Southeast Asia before utilisation of the genus by humans. This leaves open the question mentioned above, of what the natural distribution range of taro was before humans first utilised the species.

9.5 Dispersal Mechanisms: Sexual and Vegetative Reproduction

Herbarium specimens seen by the author, the author's own fieldwork, and published reports summarised and extended by Shaw (1975), Strauss et al. (1979), Sunell and Arditti (1983), and Nyman and Arditti (1985) support the view that wild taro produce flowers and viable seed abundantly throughout tropical areas of Asia and the Pacific. Experimental observations have demonstrated successful self-pollination (IITA 1978; Carson and Okada 1980), and cross-pollination (Wilder 1923; Patel et al. 1984). The morphology of inflorescences (male and female flowers separated by spathal constriction) and differential rates of male and female floral development encourage out crossing in taro (Jackson and Pelomo 1979), but self-pollination is probably also a normal event in wild populations, where pollination between flowering ramets (branches) of one clone is likely (author's observation). Inflorescences from Australian wild taro collected in 1770 can be seen in Figure 9.1. Fruit with seed, recently collected from wild taro in Australia



Figure 9.3 Inflorescences, fruit, and seeds of wild taro. *Top left*: a typical succession of inflorescences, produced from one shoot; in roadside ditch adjacent to secondary forest, Morobe Province, Papua New Guinea, June 1985. At left, a young inflorescence with spathe enclosing a spadix (not visible) which bears both female and male flowers. The upper part of the spathe turns bright yellow, releases a sweet scent, and opens slightly to admit pollinating insects. At right, an older inflorescence with upper part of the spathe completely unfurled, revealing the male portion of the spadix. At centre, an old inflorescence. The upper parts of the spathe and spadix have withered and fallen, and the remaining spathal chamber contains young fruit. Centimetre scale at base of plant. *Upper right*: young fruiting heads, one intact and the other dissected. At this stage, and at maturity, the fruit are green. Collected in rain forest at Behana Gorge, Northeast Queensland, Australia, by R. Hinxman, March 1989. *Lower left*: single ovary dissected to show the young seed within. From wild taro at Behana Gorge (details as above). *Lower right*: single mature seed taken from a herbarium specimen collected in a low-lying area of garden regrowth, near Ambunti, Sepik District, May 1966, by R. D. Hoogland and L. A. Craven (Rijksherbarium Leiden, specimen no. 226547). Note 500 μm scale bar at side. Photographed at ANU with a Cambridge Model S360 scanning electron microscope; seed coated with gold, 20 nanometres thickness.

and Papua New Guinea, are shown in Figure 9.3 Although seed germination in the wild has not been described, it is likely that most sexual reproduction occurs in the wild, where flowers and fruit can reach full maturity most easily. Throughout recorded history taro has been a vegetatively propagated crop (Nyman and Arditti 1985), and seed might reach maturity and germinate in some cultivations. This does not occur frequently because most cultivated plants are harvested before flowers or fruit reach maturity. Haudricourt (1964) suggested that new clones of taro in New Caledonia are generated by plants flowering in fallow garden areas and in the wild.

The visibly predominant form of reproduction and dispersal in the wild is vegetative, and generative vegetative parts (corms, side-corms, and stolons) are frequently dispersed

down watersheds by water, from clumps of plants growing in or next to streams, rivers, and swamps (personal observation). Natural dispersal of pollen has not been observed, but drosophilid flies are believed to be vectors for taro pollen in Asia and New Guinea (Carson and Okada 1980). Hambali (1980) recorded the dispersal of taro seed by the common palm civet of Indonesia (*Paradoxuruxs hermaphroditus* Pallus, an omnivorous, frequently arboreal mammal). Marks left by the claws and teeth of the animal were found on the peduncle (stalk below the fruit), and germinating seed were seen in the excreta. Palm civets are widespread in Asia (Hambali 1980) and absent from Australia and New Guinea.

Nothing is known about the possible dispersal of fruit by birds, and specific topographical features that might be barriers or routes for long-distance natural dispersal cannot be identified, although distances alone suggest that the major Oceanic sea gaps are likely barriers. Natural long distance dispersal between watersheds must involve seed dispersal, because the vegetative parts of taro display no physical characters that suggest that animals could transport them intact.

The observations of natural reproduction and dispersal, although limited by the brevity of field surveys to date, are essential for interpreting the present geographical distribution of genotypic variation.

9.6 Analytical Approaches for Investigating the Origins and Dispersal of Taro

The combination of field surveys and laboratory analyses of genotype first began for taro in the 1950s with the application of cytological techniques that allowed direct visualisation of nuclear chromosomes. Surveys of chromosome numbers made by Yen and Wheeler (1968) and previous workers established that while diploid taro varieties (somatic chromosome number $2n = 28$) are common in Asia and the Pacific, triploid varieties ($2n = 42$) are common only in Asia and, unexpectedly, in New Zealand. The nearest location of triploid taro outside New Zealand was found to be New Caledonia, but it was not known whether triploid varieties in these two countries were the same. Yen and Wheeler (1968) noted that triploid taro in New Caledonia and New Zealand could have been introduced from Asian sources following European colonisation in the Pacific. Matthews (1984, 1985) described the predominance of three phenotypically distinct triploid taro varieties in New Zealand today, but was unable to investigate the suggested outside sources.

Yen and Wheeler (1968) suggested that the general distributional pattern of diploids in Asia and the Pacific, and triploids in Asia, arose because cultivated diploids were introduced to the Pacific islands before cultivated triploids became common in Asia. They also suggested that the ultimate origin of the species was in India, because early reports indicated the presence of two chromosome number series in India, one of $2n = 14, 28, \text{ and } 42$, and the other of $2n = 36, \text{ and } 48$ (see Darlington and Wylie 1955; Coates et al. 1988, for summaries of early reports). Surveys by Coates et al. (1988) and others have not confirmed the existence of the second chromosome number series, nor of the $2n$

= 14 chromosome number, and the accuracy of the very early chromosome counts is now doubted (Coates, pers. comm. 1988).

Over the last four decades, analytical techniques for investigating genotypic variation have proliferated, with an accompanying progressive integration of old and new techniques. After cytological techniques achieved popularity, new electrophoretic and biochemical methods for investigating protein structure and enzymatic activity appeared, and iso-enzyme analysis became popular for evolutionary and biogeographical studies. Molecular genetic techniques developed during the last fifteen years make direct investigation of any kind of DNA possible, including genes for proteins previously investigated. Molecular and cytological techniques can be combined to visualise the positions of specific DNA sequences on chromosomes. A standardised range of molecular techniques is now available for investigating a far greater range of genotypic structure than was previously accessible by cytological or protein analysis alone.

Isozymes (Tanimoto and Matsumoto 1986) and corm proteins (Hirai et al. 1989) have been used to classify Japanese taro cultivars, but until such observations are extended beyond Japan, they cannot be easily related to the general history of the species. The present thesis represents the first application of molecular genetic techniques to the analysis of taro.

Applications of these techniques to basic questions about natural evolution, at one extreme, and for contemporary agricultural goals, at the other, are now common. The revolutionary rise of an international industry in modern agricultural genetics, with a large component of university research, has perhaps diverted attention from biogeographical studies of agricultural plants, although the two lines of work are perfectly complementary. There are many examples of molecular genetic studies of crop plant evolution exploring variation in diverse classes of DNA, notably ribosomal DNA, mitochondrial DNA, and chloroplast DNA. These studies have been based in agricultural research programmes, while the present investigation of taro is uniquely based in a programme of prehistorical research.

Molecular genetic studies with both evolutionary and geographical components have been carried out for only a few major crops. Notable examples are wheat, maize, rice, soybean, potato, and tomato, for which geographically extensive collections of germplasm were available. Much of the new information for these crops has not yet been related to social history. Prehistorians are interested in a very wide range of plant species significant as foods, medicinals, drugs, ornamentals, and sources of wood and fibre. While many of these are important crops today (taro, yam, banana, sugarcane, and sweet potato, for example), there are perhaps more which are not currently, or have never been, of major economic importance, and which are correspondingly unlikely to receive attention in agricultural research programmes.

9.7 Analysis of Ribosomal DNA

After preliminary experiments that are described in Chapter Eleven, ribosomal DNA analysis was chosen for the geographical surveys of genotypic variation in cultivated and

wild taro. Ribosomal DNA contains genes for a range of ribosomal RNA (rRNA) molecules that are incorporated into ribosomes (Figure 9.4). Ribosomes are the intracellular sites of protein synthesis, and are produced in large numbers in each cell. Often as much as 75 percent of the total cellular RNA is ribosomal RNA (Novikoff and Holtzman 1976). Most genes encoded by DNA sequences are transcribed into messenger RNAs, and these are later translated into protein sequences in synthetic reactions mediated by the ribosomes. Ribosomal DNA is thus essential to all cells in all living organisms. The nucleolus, an inclusion within the cell nucleus, is involved in the assembly of ribosome precursor particles. Nucleoli form at the chromosomal sites (loci) of the genes that code for the 18S, 5.8S, and 26S RNA molecules (Flavell and Martini 1982) and rDNA containing these genes is known as *Nor*-locus rDNA. Genes coding for rRNA were among the first genes isolated in pure form, and have been studied in detail in a very wide range of organisms (Appels and Honeycutt 1986).

In eukaryotes (which include flowering plants) one to five chromosomal locations (*Nor*-loci) contain extensive tandem arrays of repeated rDNA units, the total number of units ranging from 850 in rice to 9000 in maize. The number of rDNA units at a given locus is polymorphic within a species and in certain situations can change within a few generations. Within loci, individuals, and species, the nucleotide sequences of the ribosomal DNA repeat units are generally rather homogeneous as a result of intra-specific homogenisation processes, although the degree of homogeneity varies from one species to another. Repeat units vary in length and sequence through a range of mutational processes that include single base substitutions and sequence insertions and deletions. The units of the rDNA system are arranged in tandem, and appear to evolve in concert by as yet poorly understood mechanisms that include unequal crossing over, gene conversion, and sequence transposition between sister and non-sister chromosomes (Appels and Honeycutt 1986; Tautz et al. 1987).

The rDNA unit has component sequences which evolve at different rates (Figure 9.5). The actual rRNA genes are very similar in distantly related taxa, while regions between genes, notably the large intergenic spacer region, may show virtually no similarity between distant taxa. Because of the different degrees of variability within different regions of the repeated DNA sequences, some kind of variation can be expected in any comparison of closely or distantly related taxa, and ribosomal DNA analysis has been used for many taxonomic and phylogenetic studies in both plants and animals (Appels and Honeycutt 1986; Hillis and Davis 1986; Rothschild et al. 1986). Assessment of evolutionary relationships within closely related taxa, using the more variable rDNA regions, is inevitably complicated by frequent mutation in such regions.

Among crop plant genera, rDNA variation between varieties and species, and variation in the chromosomal locations of rDNA tandem repeats, provide chromosomal, varietal, and species markers that can be used for crop-improvement breeding programmes (examples are May and Appels 1987 for wheat; and Zimmer et al. 1988 for maize). Appels and Honeycutt (1986) list seventy-three species or genera of flowering plants in which the structure and organisation of ribosomal DNA have been studied. Although most of these are cultivated species and their relatives, very few

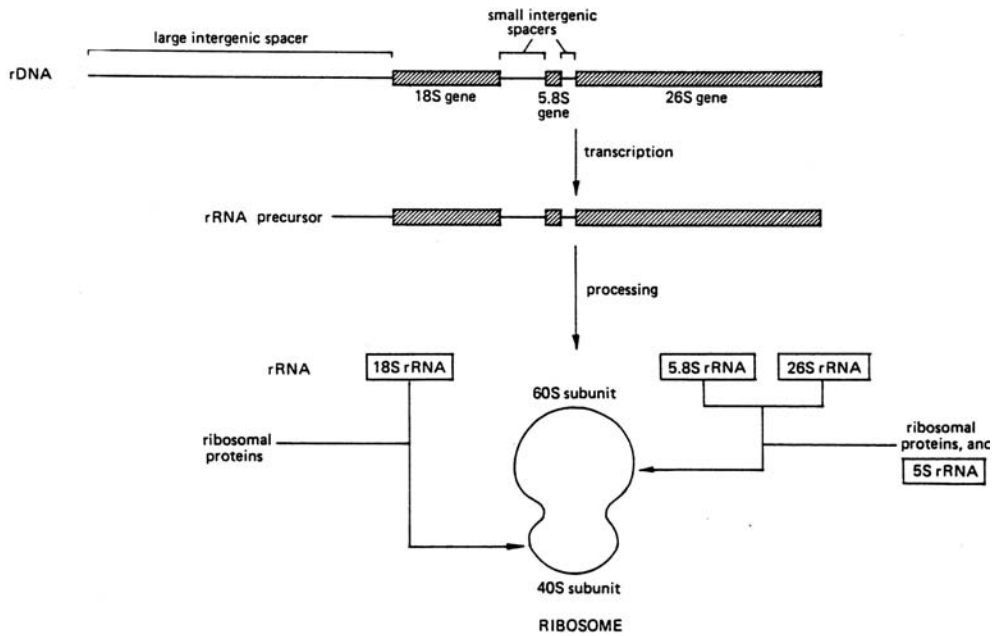


Figure 9.4 Structure and function of the *Nor*-locus ribosomal DNA repeat. Adapted from Hillis and Davis (1986)

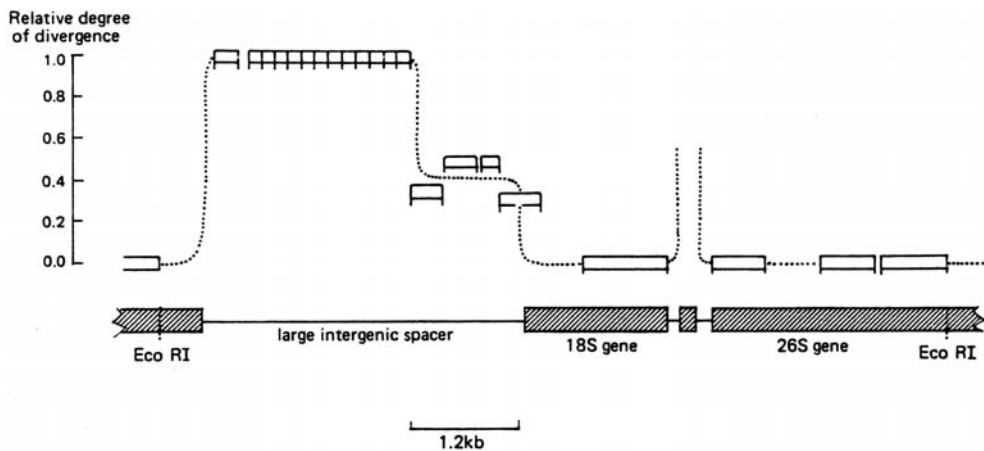


Figure 9.5 Summary of the relative degree of sequence divergence between cloned rDNA fragments from *Triticum aestivum* wheat (white blocks along upper dotted line) and four other species *Triticum*. Measures of sequence difference (thermal melting point data) were scaled relative to the maximally divergent sequences of the large intergenic spacer, and the minimally divergent sequences of the 18S and 26S rRNA genes. The asterisk, next to a break in the upper dotted line, marks a region where the exact position and degree of divergence were not determined. Adapted from Appels and Dvořák (1982b)

biogeographical studies of rDNA variation have been performed for cultivated species. The example of *Glycine* (soybean) and its relatives is of particular interest because it suggests and illustrates null hypotheses for the history of taro.

9.8 Soybean and its Relatives, and General Hypotheses for Ribosomal DNA Variation in Taro

The following summary follows Doyle and Beachy (1985). *Glycine max*, the cultivated soybean, is a major world crop today. The genus *Glycine* consists of nine species in two subgenera. The annual cultivated soybean and its wild progenitor, *Glycine soja*, belong to subgenus *Soja*. Both species are native to northeastern Asia and have diploid chromosome numbers of $2n = 40$. Seven perennial species belong to subgenus *Glycine*, which has its centre of distribution in Australia. Chromosome numbers in most of these species are $2n = 40$, but both diploids and polyploids ($2n = 4x = 80$) occur in *G. tabacina*, while a second species, *G. tomentella*, includes diploids, aneuploids ($2n = 38, 78$) and polyploids. Despite several bio-systematic studies on both subgenera, much remains to be learned about evolutionary relationships within the genus.

Ribosomal DNA was cloned from *G. max* and used to survey restriction enzyme digests of rDNA in collections of *G. max* and its relatives. Whereas heterogeneity for length and/or restriction sites was observed among small numbers of accessions in species of subgenus *Glycine*, no such variation was observed in over 40 samples of subgenus *Soja*. Sampling included accessions from throughout the native (sic = pre-modern c.f. natural range?) geographical ranges of *G. max* and *G. soja*, and a range of morphological and maturity-period types within each species. The absence of rDNA variation in subgenus *Soja* was thus thoroughly established. The species of both subgenera are inbreeders. The wild species of subgenus *Glycine* generally occur in small, isolated populations, and this, together with their breeding system, is presumably responsible for the variability observed amongst them. Human interest in the soybean, with a concomitant wide distribution of seeds and concerted efforts at plant breeding, possibly served as a homogenising force in the history of subgenus *Soja* (Doyle and Beachy 1985).

The history of taro might be similar, since putatively one species is involved, and has spread world-wide from an area of natural origin in Asia. If the general spread of taro were recent, with rapid dispersal by humans from a restricted natural distribution range, then the example of genus *Glycine* suggests that there should be little or no rDNA variation within cultivated taro. Alternatively, the natural distribution range of taro could be very wide, from eastern mainland Asia to the western Pacific, and ancient. Cultivated taro might possess very variable rDNA as a result of primary domestication processes over a wide natural distribution range in which ribosomal DNA variation was already present. Many other hypotheses can be imagined for contrast with general null hypotheses of (1) no ribosomal DNA variation in cultivated taro, (2) one area of origin of cultivated taro, and (3) a restricted natural distribution range, within the area of northeast India and Southeast Asia.

Initially, different kinds of DNA were assayed over a range of taro varieties, and in different species of *Colocasia*, using the methods described in Chapter Ten. These preliminary experiments, described in Chapter Eleven, demonstrated intra-specific variation in cultivated and feral taro, disproving the initial null hypothesis pointed above. The investigation of rDNA was therefore extended to include cultivated and wild taro from over a wide geographical range in Asia and the Pacific.

The structure and chromosomal location of ribosomal DNA in one variety of taro, described in Chapter Twelve, provide a reference point for subsequent observations of variation. Chapter Thirteen presents observations of rDNA that demonstrate the integrity of *C. esculenta* as a single taxonomic species. A survey of rDNA in diploid and triploid taro, from cultivated and wild habitats, and a wide geographical range, is described in Chapter Fourteen. In Chapter Fifteen, other kinds of biological evidence are considered in relation to the origins and antiquity of diploid taro in Australia and New Guinea, and triploid taro in Asia. Finally, in Chapter Sixteen, a general interpretation is given for the origins, dispersal, and domestication of taro.

Chapter Ten

General Materials and Methods

This chapter describes the plants studied, sample field sources, and methods for DNA analysis, including the cloning of ribosomal DNA from taro and *in situ* hybridisation analysis of the rDNA chromosomal locus.

10.1 Identification, Description and Collection of Plant Samples

Plants used in the general survey of rDNA variation are identified individually in later chapters (detailed collection records for all the plants used were held at the Australian National University until their loss in an accidental archive fire). Here, the identification, description, and collection of taro and its relatives are outlined.

10.1.1 Identification of Colocasioid genera and species

The primary text for identifying members of Subfamily Colocasioideae is Engler and Krause (1920). A simple field guide to genera and species commonly encountered in the Pacific was provided by Massal and Barrau (1956), and the classification of Family Araceae to generic level has been revised by Bogner and Nicolson (1991) and Mayo et al. (1997). In the present study, different species of *Colocasia* were identified by reference to Engler and Krause (1920), and to herbarium specimens in European herbaria. Herbarium collections of *Colocasia* and other aroids have been extensively examined and their classifications checked, in recent years, by D. Nicolson of the Smithsonian Institution. Colour plates for *Colocasia* species analysed in the present study were prepared by the author at Photo Access Co-operative (Canberra), using the Cibachrome process, as follows: *C. esculenta* (Figure 10.1), *C. esculenta* var *fontanesii* (Figure 10.2), *C. gigantea* (Figure 10.3), *C. fallax* (Figure 10.4), *C. affinis* (Figure 10.5), and *Colocasia* sp, possibly a hybrid, *C. esculenta* x *C. affinis* (Figure 10.6).

10.1.2 Description of taro varieties

A protocol for the description and agronomic evaluation of taro varieties has been published by the IBPGR Executive Secretariat (1980), but this requires 115 separate items of information, many of which are not useful for distinguishing between varieties (Jackson and Breen 1985: 14). The simplified protocol used by Jackson and Breen (1985) also is designed for agronomic evaluation, and characters recorded include time to maturity, number of suckers (side-corms), corm shape, size, palatability, consistency, aroma, dry matter content, the edibility of leaves, and the incidence of pests and diseases.

None of these characters could be consistently examined in Canberra or in the limited time available during rapid field surveys. Ten colour characters for seven parts of the plant, and a simple categorisation of growth habit, were chosen for phenotype description (Figure 10.7) after experience in the field and with potted material indicated that the characters are stable:

1. Leaf

1.1 Blade veins: anthocyanin present or absent. Note if anthocyanin is located at junction with petiole.

1.2 Blade lamina (areas between the veins): anthocyanin present or absent.

1.3 Petiole — vertically graded colours: entirely green, yellow (rare), or anthocyanin pigmented; or a graded range from green to anthocyanin pigmented. Note if anthocyanin is located at junction with blade.

1.4 Petiole — variegation (stripes and/or flecks): present or absent. If present, the variegation may be green/white (only chlorophyll pigments involved), anthocyanin variegation against a background of green or white, or a complex mixture of chlorophyll and anthocyanin variegation.

2. Basal ring: white, green, or with anthocyanin. At the base of the petiole, under the sheath of the previous leaf, the dominant colour of the epidermis is usually white, leaving the basal ring distinct, but occasionally petiole epidermal colour extends to the base, obscuring the anatomically deeper colour or the basal ring.

3. Roots: white or with anthocyanin.

4. Skin (living epidermis of the corm below the outer layer of brown, decayed, epidermal and leaf tissue; scrape with knife to examine): white or with anthocyanin. 5. Cortex parenchyma (view in cross section of corm; the tissue between the skin and the zone of root initials): white, or with anthocyanin.

6. Core parenchyma (view in cross-section of corm; the entire region inside the zone of root initials): white, carrot orange, mustard yellow, or with anthocyanin. White includes faintly yellow, creamy colours, distinct from mustard yellow tints. Rarely, sectors of white and purple parenchyma were recorded, with a corresponding variegation of the corm skin.

7. Corm core fibres: colourless, white, yellow (usually very pale), or with anthocyanin.

8. Growth habit (lateral shoots): side-corms, direct shoots, or stolons. Stolons are defined here as side-shoots with at least one node and two internodes separating the mother corm and the lateral apex.

A range of presumed anthocyanin-based colours were observed: pink, red, purple, bronze (a mixture of purple and green), and black. This last, most intense, pigmentation was found only on petioles. Colour variants of taro arising during vegetative growth have been reported (e.g. Whitney et al. 1939: 46–47), but not in detail. Vegetative mutation of general colour pattern or morphology was not observed during the present study.

Detailed records of varietal differences in the size, shape, clustering, and number of central and lateral shoots were not made, since these are significantly affected by environmental conditions. Shoots growing directly from the central corm are not very

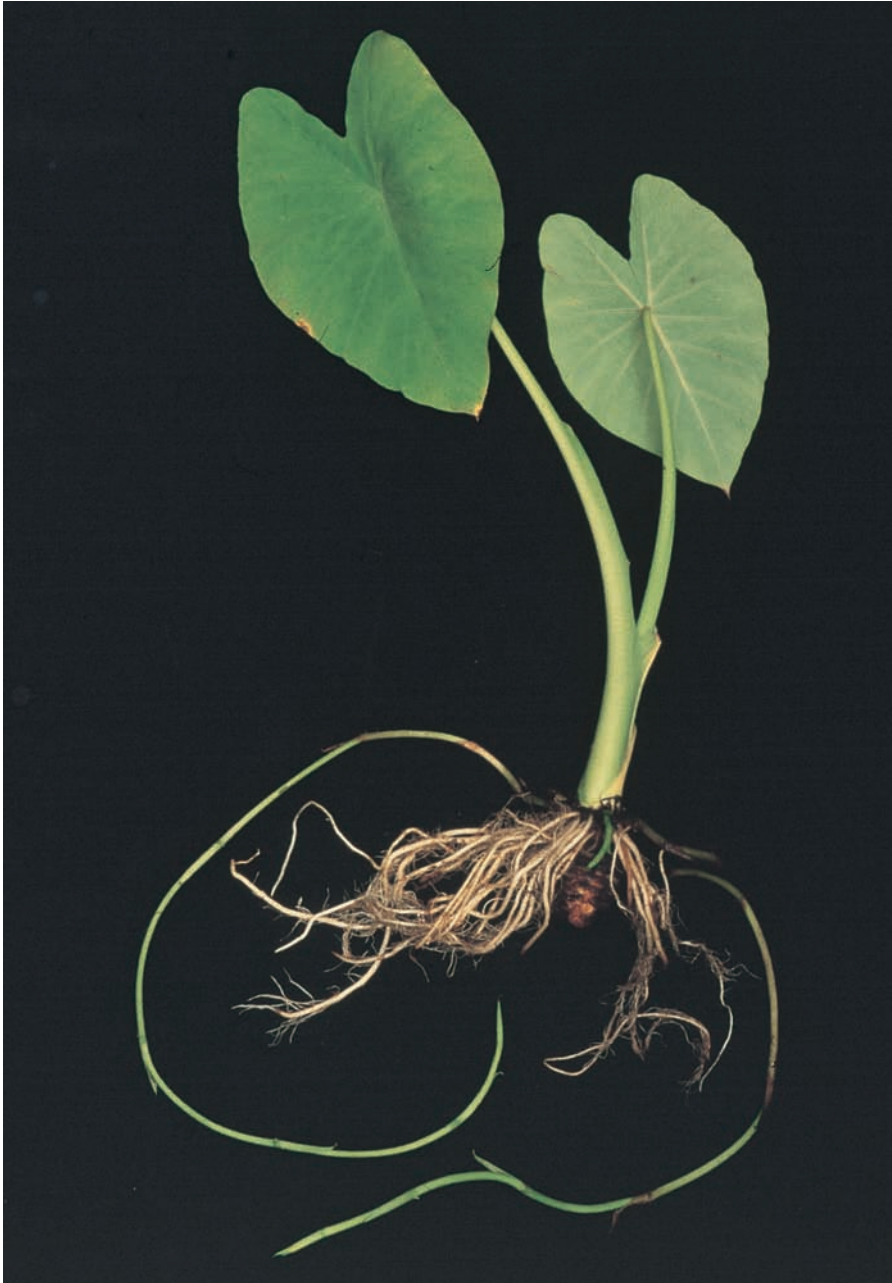


Figure 10.1 *C. esculenta* (L.) Schott from wild, tropical rainforest habitat, Russell River, northeastern Queensland, Australia. Phenotype typical for Australian wild taro: leaf blade with green veins and lamina; green petiole with no variegation; white basal ring; white roots; corm with white skin, white cortex parenchyma, white core parenchyma, yellow fibres, and small with a low density of starch: vegetative growth habit stoloniferous (potted plant maintained in Canberra). Chromosome number: $2n = 28$. Wild taro in coastal Morobe Province, Papua New Guinea, displays a similar phenotype. Scale: plant approximately 0.5 m high (length of the larger petiole)

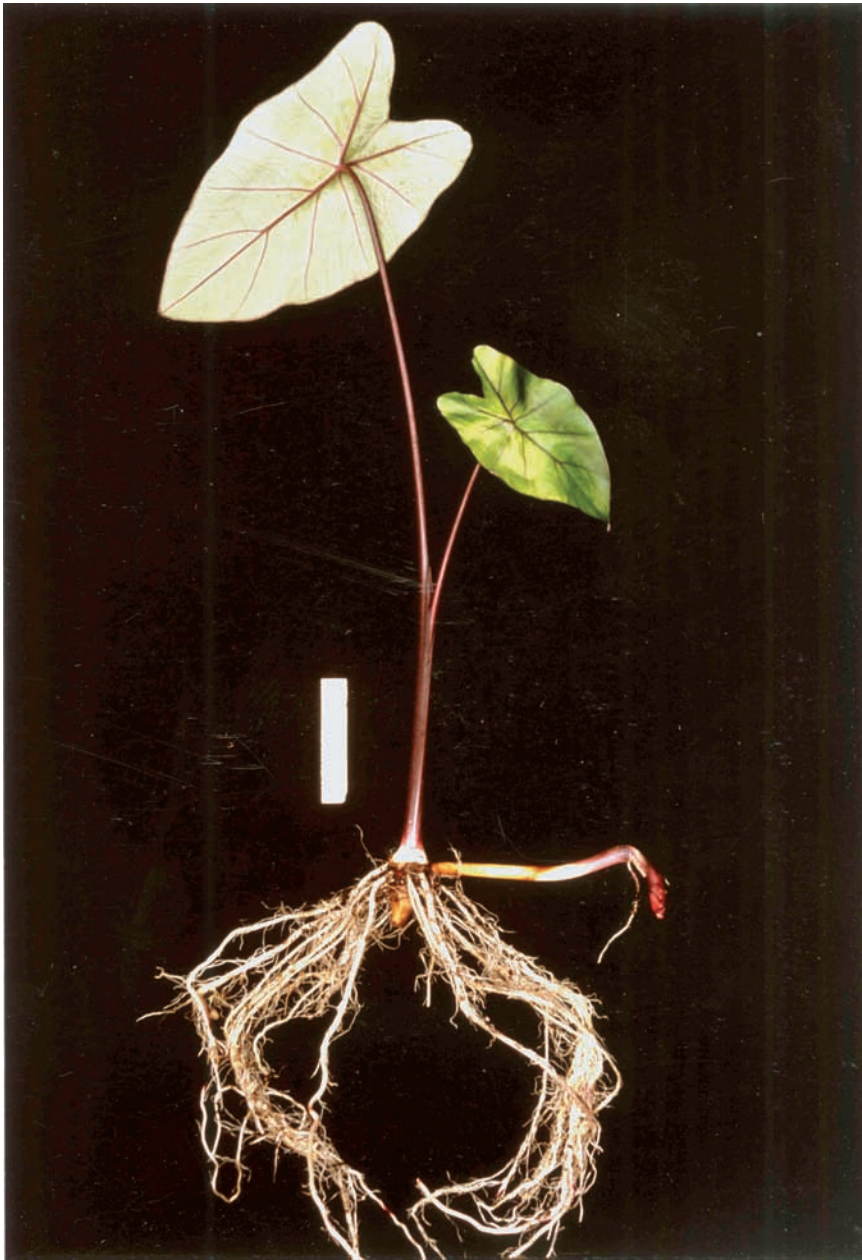


Figure 10.2 *C. esculenta*, var. *fontanesii* (Schott) A. F. Hill comb. nov., from wild lakeside habitat, inland mountain forest, Eliya, Sri Lanka (potted plant maintained in Canberra, T322). Not seen elsewhere in vicinity of the collection site; phenotype same as that of plants commonly grown as ornamentals in Australia and New Zealand: purple veins, purplish lamina, purple graded petiole colour, no variegation; white basal ring; white roots; corm with white skin, white cortex parenchyma, white core parenchyma, and yellow fibres; growth habit stoloniferous. The upper surface of the leaf blade has a distinctive shiny appearance and leathery texture. Chromosome number: $2n = 42$. Scale bar: 5.5 cm

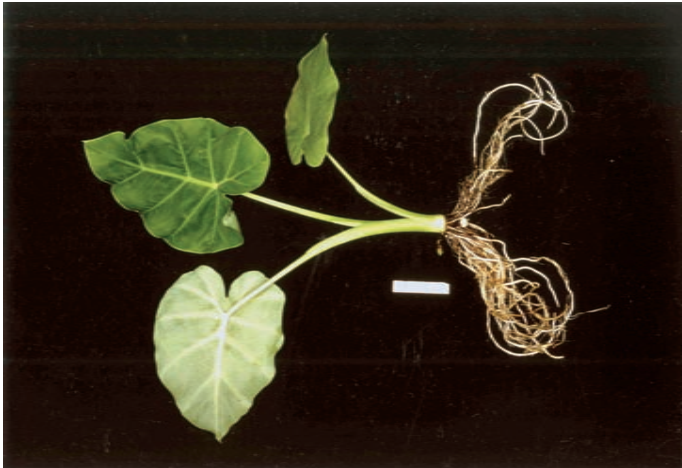


Figure 10.3 *C. gigantea* Hook, f., from Brisbane, source outside Australia not known. One-year-old seedling (T387.33) grown in Canberra from seed produced spontaneously, outdoors, in the Brisbane Botanic Gardens. White to green veins, green lamina, green petiole without variegation; white basal ring; white roots; corm with white skin, white cortex parenchyma, white core parenchyma, and yellow fibres, growth habit stoloniferous. Leaf veins in this species are more broadly spaced than is typical of *C. esculenta*, and the seed and inflorescence are also distinctive. Chromosome number: $2n = 28$. See also Figure 18.1.

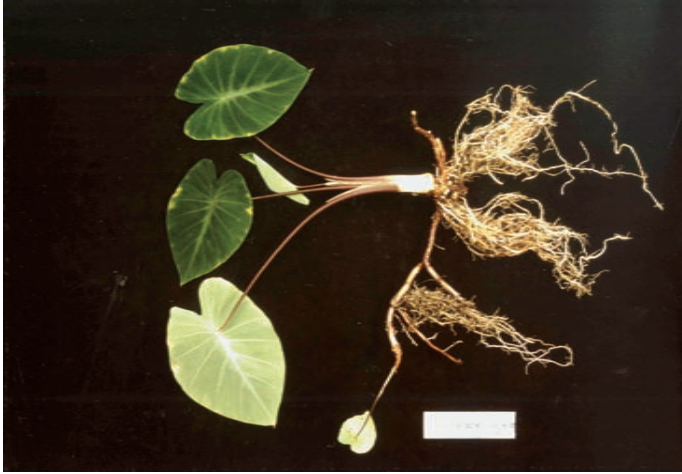


Figure 10.4 *C. fallax* Schott from Rockhampton, Australia, where it was grown as an ornamental (potted plant maintained in Canberra, T269; source outside Australia not known). Green veins, green lamina, purple petiole without variegation, white to green basal ring; white roots; corm with white skin, green to yellow cortex parenchyma, green to yellow core parenchyma, and colourless to yellow fibres; growth habit stoloniferous. The corm is a short narrow stem, almost woody, with a low density of starch. The lack of white colour probably reflects the lack of starch. The green to yellow colours probably represent environmentally induced variation in plastid development within the corm parenchyma. The upper leaf surface of this species has a matt sheen not found in *C. esculenta*, and the inflorescence is also distinctive. Chromosome number: $2n = 28$

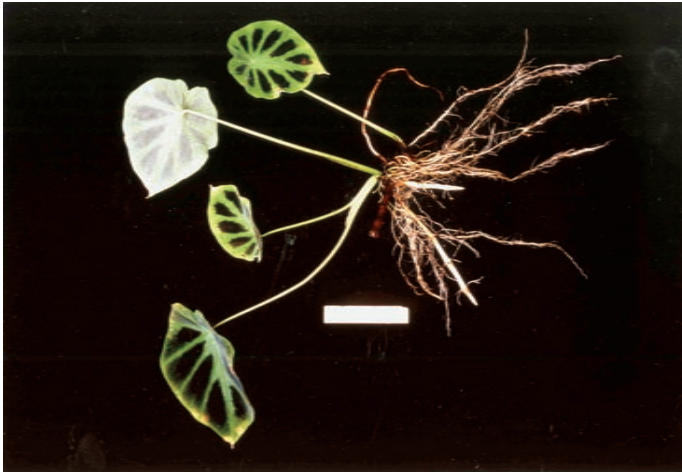


Figure 10.5 *C. affinis* Schott, var. *jenningsii* (Veitch) Engler, from cultivation in England (potted plant maintained in Canberra, T328; source outside England not known). Green veins, purplish black patches on lamina, green petioles without variegation, white basal ring; white roots; corm small with white skin; growth habit stoloniferous. The leaf colour pattern of this variety of *C. affinis* is not found in *C. esculenta*. Scale: 5.5 cm

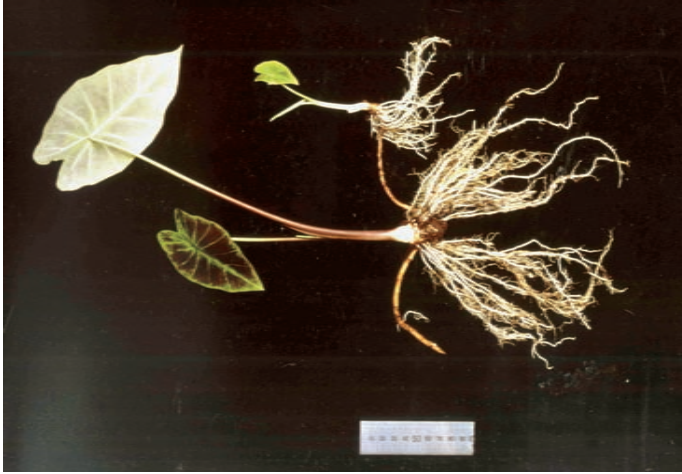


Figure 10.6 *Colocasia* sp. (*C. affinis* x *C. esculenta*?), c.f. *C. marchallii* Engler; from Rockhampton, Australia, where it was grown as an ornamental (potted plant maintained in Canberra, T270; source outside Australia not known). Veins white to green, lamina purple edged with green, petiole green grading into purple without variegation, basal ring white; roots white; skin white, cortex white, fibres yellow; growth habit stoloniferous. Both the colour and the elongate shape of the blade distinguish T270 from *C. esculenta*. Chromosome number: $2n = 28$ (P. J. Matthews count)

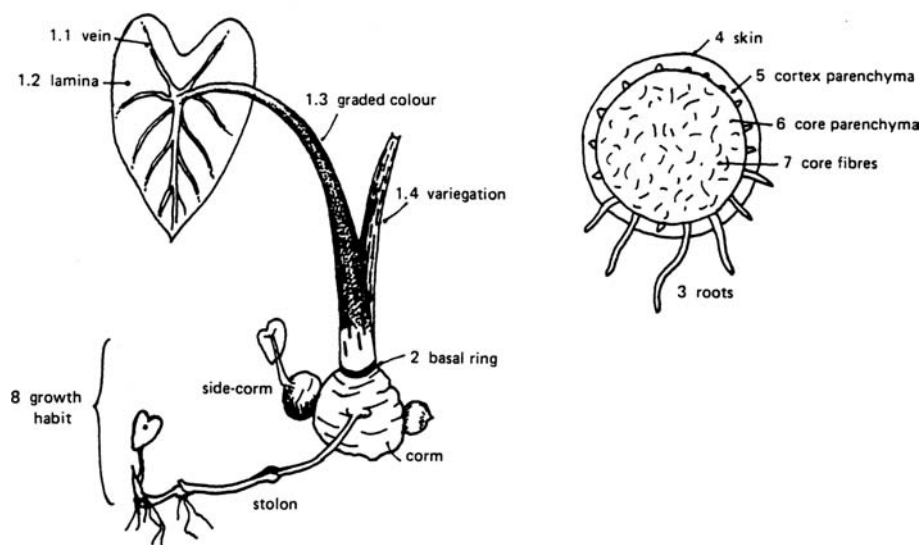


Figure 10.7 Characters for phenotype description of taro: 1.1–1.4 = leaf characters; 2 = basal ring; 3 = roots; 4–7 = central corm characters; 8 = growth habit (lateral shoots). The corm characters are illustrated in cross section (right). Side-corms and stolons are distinct character states which do not occur on the same plant. See text for descriptions of character states

common, and may or may not be environmentally induced. The two major categories of lateral shoot formation, side-corms and stolons, are consistently expressed under both field and glasshouse conditions.

Phenotypes were recorded (1) in the course of fieldwork, (2) for cross-checking the labels of accessions maintained in Canberra, and (3) to allow comparison of phenotypic and genotypic variation (Chapter Fourteen).

10.1.3 Field Surveys and collections

Exploratory fieldwork by the author was required to obtain wild taro from Morobe Province, Papua New Guinea (June–July 1985) and Queensland, Australia (September–October 1987). The geographical distributions and habitats of varieties collected in New Zealand were described by Matthews (1984, 1985). Further specimens of wild taro, mainly Australian, were received from various collectors, and most cultivated taro specimens were received directly from other collectors or from existing cultivar collections (Appendix 15). All plants received from outside Australia were introduced via the Australian Government Plant Quarantine Station at Weston Creek, Canberra, ACT.

Wild taro are widespread in Melanesia, but are rarely mentioned in ethnographic, agricultural, and botanical accounts. Treide (1967) discusses the role of wild plants as food in Melanesia generally, and cites Guppy (1887) for a record of taro growing wild

on river banks and in mountain ravines on islands in the Strait of Bougainville, Solomon Islands. Wild taro are common today in streams and swamps of the Solomon Islands generally (Patel et al. 1984; Spriggs pers. comm. 1989; Roe pers. comm. 1989). Henderson and Hancock (1988) note that the leaves and corms of wild taro, in the Solomon Islands, are usually too irritant to be edible. A wild variety on Rennell Island has an edible but fibrous corm, classed as a scarcity food, and the leaves of a wild variety in Malaita are collected as a vegetable. Within mainland New Guinea, wild taro have been reported across a wide geographic range. Bulmer (1968) notes feral *C. esculenta* as very plentiful in streambanks at 600 to 900 m and reaching 1500 m, among plants present in the Kaironk Valley region, Western Highlands, before European contact. Carson and Okada (1980) describe insects associated with wild taro which they found growing in rivers, streams, and along roadsides, near Lae, Morobe Province. Hyndman (1982) lists the leaves of wild taro, '*Colocasia* sp.', presumably *C. esculenta*, as a leaf vegetable obtained from foothill rain forest (500–1000 m) in the upper Fly River district of central New Guinea. In a survey of herbarium collections in Europe, Australia, and Papua New Guinea, only five records of wild taro in Papua New Guinea were obtained (Appendix 16), of which four were reported as being stoloniferous: on the Palmer River, Fly District; at Sogeri, near Port Moresby; at Nanokawari, West New Guinea; and at Buimo Creek near Lae, Morobe Province. The growth habit was not described for wild taro found near Mount Hagen and Mount Kuta, in the Western Highlands.

In 1985, wild taro were surveyed in the vicinity of Lae, Morobe Province, Papua New Guinea (Figure 10.8). In the lowland area surveyed, rainfall, temperature, and humidity are high throughout the year (McAlpine et al. 1983), and the wild taro occupy open, forest fringe habitats where both light and water are available (Figure 10.9). Although no clear distinction could be made between feral taro recently escaped from gardens and self-propagating wild taro, a high degree of phenotypic uniformity was noted among wild taro in sites that were not immediately adjacent to current gardens. Flowering was widespread. The commonly observed phenotype (Figures 10.1 and 10.10) consisted of a predominantly green blade and leaf, with a variable degree of purple colouring at the junction of blade and petiole, no variegation, a white basal ring, white roots, a vigorous stoloniferous growth habit, and a corm with very little starch (non-starchy). Throughout the area shown in Figure 10.8, village gardens contain various combinations of banana, sweet potato, yam, and taro. Under cultivation, the altitudinal range of taro in Papua New Guinea extends to 2700 m (Bourke 1982). The 1985 survey of wild taro was confined to altitudes of 1000 m and less, well below the potential altitudinal range for cultivated taro. It is thus possible that wild taro of the sort described above has a greater altitudinal range than recorded so far.

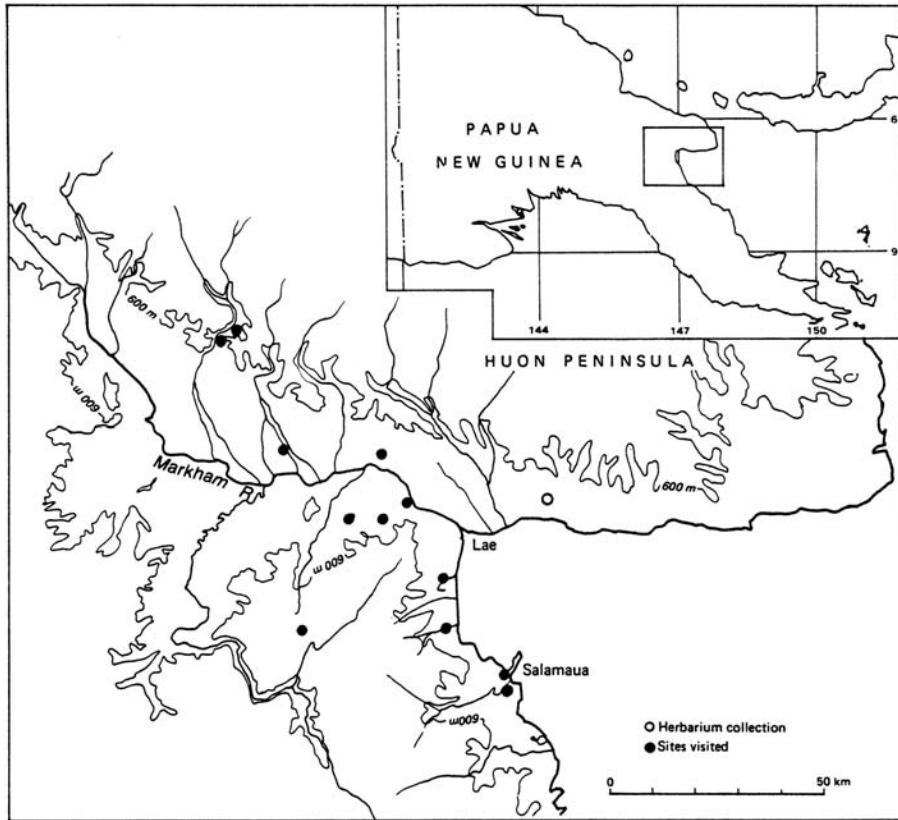


Figure 10.8 Locations of stoloniferous wild taro in Morobe Province, Papua New Guinea, July to August 1985. The search was limited to the vicinity of Lae, from Salamaua to the middle tributaries of the Markham River. One herbarium record is included (1964165 collection by A. Jenny). The sites are described in Appendix 16.



Figure 10.9 Wild taro, Morobe Province, Papua New Guinea (photos from Matthews 1987; see Appendix 16 for site details). Above: Pipi stream, near Labutali village, on coast between Lae and Salamaua, 16 July 1985; plants with long surface stolons, blade green with purple colour at junction to petiole, petiole green without variegation, basal ring white; inflorescences of various maturity, including some with young fruit and seed. Specimens of *Colocasiomyia pistilicola* Carson and Okada, a fly that probably pollinates taro, were collected from inflorescences at this site (see Figure 15.1). Below: Stream bank in forest near Nariyawan village, Leron River, inland tributary of the Markham River, 5 July 1985; a few metres from a foot track to mixed-crop gardens with taro. Phenotype like that described above, but not flowering (*in situ* photograph of Canberra live collection T225).



Figure 10.10 Wild taro photographed with alluvial mud at collection site, Rumu River, Morobe Province, Papua New Guinea; 29 June 1985 (*in situ* photograph of Canberra live collection T229). Blades and petioles green, basal ring white with coarse white roots, here cut short for the photograph, and non-starchy corms arising from stolons; wider than the base of the petiole. This phenotype is common among wild taro in Morobe Province, and wild taro in Australia display a similar phenotype. Scale bar: 15 cm



Figure 10.11 General distribution of wild taro in Australia, based on records from 1770 to 1989 (Appendix 17). Dark grey areas are where taro were recorded, and the light grey area indicates the possible full distribution range, within the climatic zone of tropical summer rainfall.

Records of wild taro in Australia are restricted to the climatic zone of tropical summer rainfall (Figure 10.11). The taro are widely distributed but generally rare, with highly localised patches associated with permanent water, in the Kimberley region of Western Australia (K. Kineally and S. Forbes pers. comm. 1985), Arnhem Land, Northern Territory (R. Jones pers. comm. 1989), and the Kakadu region, Northern Territory (Russel-Smith 1984). Exploration of the wet, tropical rain forest zone of northeast Queensland was undertaken because early ethnographic and botanical records and reports from correspondents indicated that wild taro is relatively common there (Appendix 17) and because access was easier than in the northern areas.



Figure 10.12 Wild taro in northeast Queensland: sites recorded between late 1987 and late 1989. One variety (Jiyer phenotype) was found in natural and disturbed habitats over the entire range shown. Historical records (Banks 1770, Bailey 1889) and site details are noted in Appendix 17.

Within the last twenty years (1970–1989), twice as many records have been made as in the previous 200 years (Table 10.1). The two least-accessible areas, Western Australia and Northern Territory, provide three-quarters as many records as the more accessible area, Queensland, although recent helicopter surveys by botanists are changing this balance (P. Latz pers. comm. 1989). During the last two years (late 1987 to late 1989) the specific search for taro in northeast Queensland yielded twenty-one records (Figure 10.12), as many as all previous records for this area. The small total number of records for Australia seems largely attributable to geographical remoteness. It is not known to what extent wild taro have been damaged by cattle and wild pigs. More damage is likely to be caused by cattle at permanent water holes in the drier northern areas.

The arid climatic zone (Figure 10.11) presents an unbroken southern barrier for taro in western and central Australia. In eastern Australia, the zone of subtropical summer rainfall does not impose any obvious, broad-scale, environmental limitation on the dispersal of taro. Three possible reasons for the lack of records south of Townsville can be suggested. First, natural short-distance dispersal and establishment could be prevented by the pockets of aridity that extend inland from the coast between Townsville and Bundaberg. Secondly, the ranges of animals and insects responsible for natural dispersal (if any) could be limited by climatic conditions, even though the plant is not. Thirdly, if humans have been responsible for dispersal, then unknown historical and cultural factors may have been involved which did not apply to the wide dispersal of taro across the top end of Australia. The area between Ingham and Cairns (Figure 10.12) competes with western Tasmania for the highest recorded rainfall in Australia, experiencing median annual rainfalls of 2400 to 3200 mm (Bureau of Meteorology 1986). The highest recorded altitude for a taro site in Australia, at c.980 m, is in this tropical, high-rainfall area at Cannabullen Falls on an inland tributary of the Tully River (B. Hyland collection, 27 March 1966; Appendix 17). Other sites approaching a similar altitude were recorded

Table 10.1 Summary of records for taro in Australia, 1770–1989, based on Appendix 17

	1770–1969	1970–1989	Totals
Western Australia	1	10	11
Northern Territory	4	17	21
Queensland	18	28	46
Unknown location	2	0	2
Totals	25	55	80

All or most of the records in this summary, and in Appendix 17, represent wild taro. Although most early reports do not indicate whether the plants were wild or cultivated, wild taro can generally be inferred because of an early date, prior to the institution of gardening by recent immigrants, or geographical remoteness. The summary excludes one uncertain but very early record by Leichardt (1847), and a repeated visit to one location by N. White (18 August 1983). Included in the summary are the different locations reported by Bailey (1889) and Roth (1901).

on the Atherton Tableland between Rockingham Bay and Cairns, during the period 1987 to 1988.

10.1.4 The Canberra Taro Collection

A living collection of taro was first established in Canberra in 1981 by D. E. Yen, with additions made continuously thereafter. Most of the collection was dispatched in 1989 to the Department of Botany, University of Selangor, Kuala Lumpur, Malaysia, and a representative range of Australian accessions was left with the Australian National Botanic Gardens in Canberra.

Taro plants are generally robust and survived well the process of field collection, transport, quarantine, and maintenance in Canberra. For international air transport, all soil was removed from the plants by washing in water, leaves were cut above the sheath of the outermost leaf, corms were cut two or more centimetres below the apex, and roots and rotting parts were removed. For transport, stolons were cut into conveniently sized sections, usually with at least two nodes each. Actively growing shoots were packaged in slightly damp cotton wool after dusting corm surfaces with sulphur. Dormant shoots (from temperate Japan) were packaged in dry paper. The shoots were wrapped with labels and placed in unsealed plastic bags with further labelling outside.

For maintenance in Canberra, the collection was kept heated and covered with glass or plastic at the Australian National Botanic Gardens and at the Research School of Biological Sciences. In summer, some plants were kept outside under shade cloth. The plants were grown in standard, sterile potting mixtures of peat, soil, pumice, and river sand, in plastic pots. Propagation was entirely by vegetative parts, generally corms, side-corms, direct side-shoots, or the nodes of stolons. Growth was strongest in summer and was encouraged by repotting, additions of fertiliser (Osmocote slow-release pellets), and by standing the potted plants in shallow trays of water. During the months of decreasing and short day-length leaves emerged slowly and decreased in size. Some accessions stopped growing completely. In winter, the plants were removed from trays and given less top watering and fertiliser. Fungal rots and garden slugs were the two most common causes for loss of accessions. Repotting, duplicate planting, encouraging active growth, and poison slug baits helped to reduce losses. White flies, aphids, and red spider mites were significant insect pests, particularly in late summer. Top watering and insecticide sprays achieved partial control of these. Plants that developed viral symptoms after quarantine were discarded after sampling for laboratory analysis.

10.2 Laboratory Methods

Sterile equipment and distilled water were used for all protocols. Frequently used stock solutions are described in Appendix 19.

10.2.1 Leaf harvest

For one DNA extract, leaves were harvested from one or more shoots of one clone. Clones were identified in the field by physical connections between shoots, and shoots

belonging to one clone were maintained in the Canberra collection under one accession number.

The best yields of DNA were obtained from leaves taken just before or just after emergence from the sheath of the preceding leaf (Figure 10.13). Leaves at this stage are usually yellow green or pale green, or visible by looking for the tip of the young leaf within the top part of a recently opened sheath. To remove the leaf, a thumbnail or blade was used to cut the petiole under and along the sheath, then to pull out the young leaf, detaching blade from petiole at the blade-petiole junction. Petioles yield little DNA and interfere later with smooth grinding of the frozen leaf blade. Very young leaves are yellow and yield less for their fresh weight. Older, emerged leaves also can be used, particularly any softer, immature portions, but the yield of DNA per gram of fresh tissue is less. It was not always possible to obtain an ideal leaf, and yields varied in the order of 100 to 1000 $\mu\text{g/g}$ fresh weight. A good yield sufficient for several tests could be expected from a single young leaf 10–15 cm, in the immature rolled state, and weighing 1–2 g. After harvest, leaves were kept on ice for DNA extraction the same day. For longer storage (indefinitely) leaves were wrapped in aluminium foil with labels inside and out, and stored at -70°C or in liquid nitrogen (-176°C). Portable steel vacuum dewars were used for storing leaf samples in liquid nitrogen in the field (Queensland). For DNA extraction, the frozen leaves were removed from storage without allowing them to thaw. For sorting and unwrapping, deep-frozen samples were transferred to a small polystyrene container containing liquid nitrogen.

10.2.2 Extraction and purification of total DNA from leaves

A procedure similar to that described by Appels and Moran (1984) was used:

(1) Place 0.5–2 g of young leaf tissue in a mortar containing liquid nitrogen and approximately 1 g of acid-washed sand. Grind to a fine powder, using further liquid nitrogen to prevent thawing.

(2) Transfer powder to a second mortar, at room temperature, containing 6–8 ml of buffer (40 mM Tris.HCl, 80 mM NaCl, 160 mM Na EDTA, 0.5% SDS w/v, 0.05 mg proteinase-K/ml, pH approximately 7.5), freshly made by mixing 8 parts *stock leaf DNA extraction buffer*, 1 part 5% SDS (w/v H_2O), and 1 part fresh proteinase-K solution (0.5 mg/ml). Grind immediately but gently to ensure rapid penetration of the buffer.

(3) Transfer the viscous slurry to a 50 ml Nalgene polycarbonate tube, or other suitable tube, and incubate at 37°C for 1–3 hours while processing further samples.

(4) Add 1 g sodium perchlorate to each tube, dissolve by vortexing briefly.

(5) Balance tubes with either sand or *stock leaf-DNA extraction buffer*. Centrifuge to remove debris: 8000 rpm, Sorvall SS34 fixed-angle rotor, 5–8 minutes, RT or cold (e.g. 8°C).

(6) Transfer supernatant to clean tube, then gently add 9 ml of 70% ethanol saturated with sodium perchlorate (*EPR stock solution*), at RT. Mix gently with slow inversions to assist precipitation of DNA. The DNA precipitates may be white, yellow, or green, and stringy or cloudy. Stringy precipitates have DNA that is more intact, and are better than cloudy precipitates.

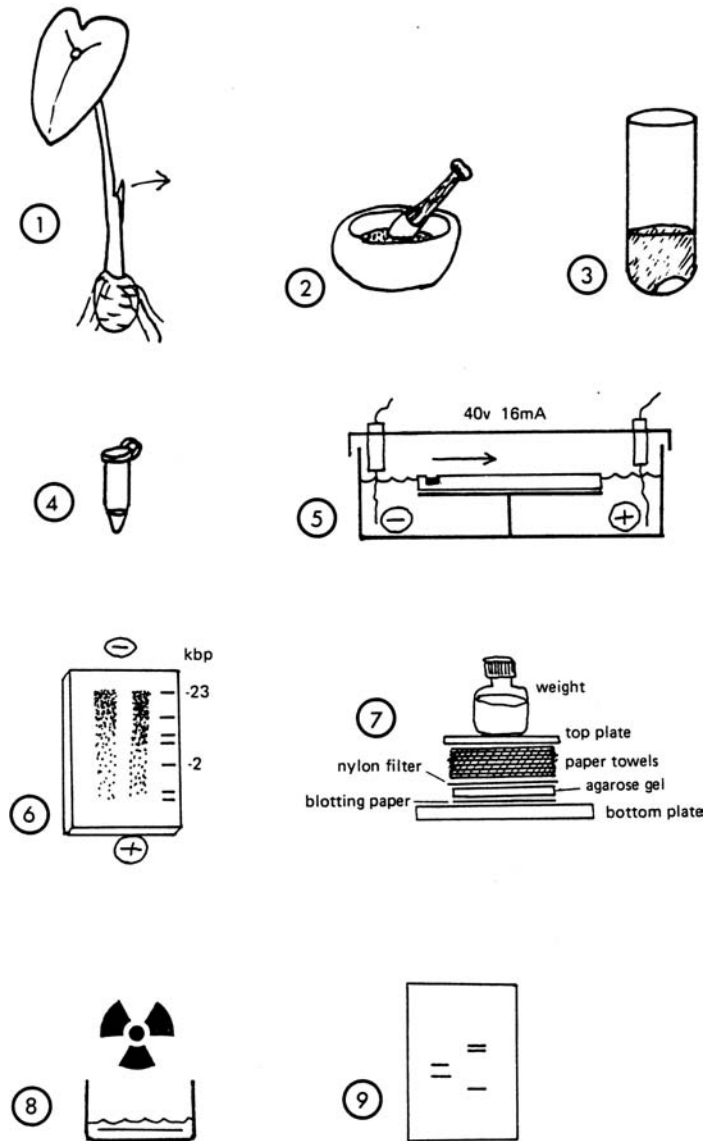


Figure 10.13 Schematic outline for DNA analysis: (1) harvest of young leaf, (2) reduction of tissue to powder by grinding in liquid nitrogen, (3) lysis with detergent and proteinase (enzyme), and further purification, (4) digestion of the DNA, in microgram amounts, with restriction enzymes, (5) electrophoresis in buffered salt solution after loading the reaction mixture onto an agarose, horizontal-slab gel, (6) visualisation of DNA samples and size standards (kilobase pairs) with ethidium bromide staining and UV light, (7) Southern transfer of DNA fragments to a nylon filter, by capillary fluid flow into paper towels, (8) incubation of the filter in hybridising solution with radioactively labelled DNA probe, (9) X-ray autoradiography, after washing to remove probe DNA that did not hybridise with the target leaf-DNA fragments.

(7) Remove stringy precipitates by winding on a sterile Pasteur pipette, retrieve cloudy precipitates by centrifugation: 8000 rpm, Sorvall SS34 fixed-angle rotor, 5–8 minutes, RT or cold.

(8) Resuspend the DNA in 0.4 ml (or multiples of 0.4 ml if pellet is large) of *stock 50 TE 20(8)*, in a 1.5 ml Eppendorf tube. Leave overnight at 4°C, if desired.

(9) To each 0.4 ml of resuspended DNA, add 0.2 ml *stock phenol* and 0.2 ml *stock chloroform*. To completely remove proteins and colour from the DNA, leave the mixture for several hours or overnight, at 4°C, without shaking. Spin 1 minute with bench centrifuge.

(10) Transfer the colourless, aqueous, upper phase to a fresh 1.5 ml Eppendorf tube and precipitate with 0.8 ml *stock ethanol and sodium acetate solution*, at RT. Store overnight or longer at 4°C or -20°C, if desired.

(11) Spin ethanol precipitate for 5–10 minutes with bench centrifuge. Discard supernatant and wash pellet with approximately 0.5 ml 70% ethanol. Dry moderately, then resuspend with 0.4 ml of *stock 10 TE 1(8)*. Leave overnight at 4°C and use Pasteur pipette to assist resuspension, if necessary.

(12) Add 2 ul of *stock boiled RNA'se A* (10mg/ml, Boehringer) to give a final concentration of 50 ug/ml. Incubate 20 minutes at 37°C.

(13) Add 45 ul of fresh proteinase-K solution (1 mg/ml) to give a final concentration of 100 ug/ml. Add 4.5 ul of 10% SDS to give a final concentration of 0.1% w/v. Incubate 20–30 minutes at 37°C.

(14) Add 0.2 ml *stock phenol* and 0.2 ml *stock chloroform*, shake vigorously, and spin immediately: 1 minute with bench centrifuge.

(15) Transfer aqueous phase to fresh 1.5 ml Eppendorf tube and precipitate with 0.9 ml *stock ethanol and sodium acetate solution*, store overnight or longer at 4°C or -20°C, if desired.

(16) Spin for 10 minutes with bench centrifuge. Discard supernatant and wash pellet with approximately 0.5 ml 70% ethanol. Dry moderately, then resuspend in an appropriate volume of *stock 10 TE 1(8)*, according to visible size of the pellet. Standardise resuspension volumes to assist routine estimation of DNA yield, later, e.g. 100 ul, 200 ul, or 400 ul.

10.2.3 DNA concentration and quality

Highly variable yields of lead DNA were obtained because the starting materials were not completely uniform. The bulk of total DNA extracted from leaves consisted of fragments in the 20–30 kbp size range, sufficiently intact for all requirements in the present study. DNA yields also varied with each bacterial culture if recombinant plasmid (methods described later). The following protocol was used to give DNA extracts of known concentration, and for quality checks:

(1) Estimate concentration by diluting 10 ul of each sample in 990 ul H₂O, and reading the optical density at 260 nm and 280 nm with a spectrophotometer. Calculate the approximate concentration for each sample, assuming that an extinction coefficient of OD 260 = 20 corresponds to 1 ug double-stranded DNA/ul (Maniatus et al. 1982: 458).

(2) Using the first estimate of concentration, electrophorese a standard quantity of each extract (e.g. 1 ug) on an agarose gel, stain with ethidium bromide, and photograph. Use visual comparison with a commercially supplied DNA sample of known concentration (e.g. intact lambda DNA) to check for under- or over-estimation. This step can also be used to check the degree of DNA degradation after extraction, and the amount of RNA accompanying the DNA. Estimate yields and adjust volumes with *stock 10 TE 1(8)* to give a final concentration of 1 ug DNA/ul. For extracts which require a smaller volume, precipitate the DNA with ethanol and sodium acetate, then resuspend.

Leaf DNA extracts which were yellow or yellow-brown after extraction and purification were often poorly cut by restriction enzymes. Because of the differential absorption of light by DNA and other compounds, the optical density ratio of OD 260/OD 280 indicates the degree of nucleic acid purity. Pure DNA gives a ratio of 1.8 (Maniatus et al. 1982: 468). Contamination with RNA raises the ratio towards 2.0, while contamination with protein or phenol lowers the ratio. The protocol for leaf DNA extraction, above, usually gave extracts with ratios in the range 1.6–1.9. Such extracts were reliably cut by restriction enzymes. Extreme values of c.a. 1.3 and 2.2 also were observed. Ratios above 1.8 indicate RNA, which does not interfere with restriction enzymes; ratios below 1.6 indicate contaminants, notably phenol, which may interfere with restriction enzymes; and at both extremes of optical density ratio, the amount of DNA present cannot be estimated accurately with the OD 260.

10.2.4 Propagation, extraction and purification of plasmid DNA

Various recombinant plasmids containing mitochondrial ampicillin resistance were propagated in *E. coli* on agar or in liquid, using Luria-Bertani (LB) medium with ampicillin. Mini scale extracts of plasmid DNA were prepared by alkaline lysis for screening plasmids after ligation with taro DNA fragments, and to create stocks of previously constructed and defined recombinant plasmids. Large-scale plasmid extracts were prepared by alkaline lysis of purification on caesium chloride gradients. Highly purified plasmid DNA was used to prepare radioactive probes and for restriction enzyme analysis. The protocols for plasmid propagation, extraction, and purification are essentially as described by Maniatus et al. (1982).

Mini-scale alkaline lysis

(1) Use a single, fresh bacterial colony from an agar plate to inoculate 2–5 ml of *stock LB medium* with ampicillin (50mg/l). Incubate for 5 hours to overnight at 37°C with vigorous shaking. Alternatively, streak a single colony onto a fresh LB agar plate, with ampicillin (50 mg/l), and incubate overnight at 37°C.

(2) Transfer 1.5 ml of liquid culture to a 1.5 ml Eppendorf tube and spin for 1 minute with bench centrifuge. Discard supernatant, and drain well or aspirate.

(3) Resuspend pellet by vortexing with 100 ul of ice-cold *stock GET solution* (50 mM glucose, 10 mM Na₂EDTA, 25 mM Tris.HCl, pH 8.0). Alternatively, take 1–2 platinum wire loops of cells scraped from an overnight agar plate culture, and resuspend in 100 ul of ice-cold *stock GET solution*. Stand tube at RT for 5 minutes.

(4) Add 200 μ l of a freshly made solution of 0.2 M NaOH, 1% SDS, mix contents by inverting the tube rapidly two or three times, do not vortex. Stand tube on ice for 5 minutes.

(5) Add 150 μ l of ice-cold *stock 3M potassium, 5M acetate*. Invert tube and vortex gently for a few seconds, until well mixed. Stand tube on ice for 5 minutes.

(6) Spin for 5 minutes with bench centrifuge, 4°C. Transfer supernatant to fresh 1.5 ml tube. Add 200 μ l each of phenol and chloroform. Vortex briefly and spin 1 minute with bench centrifuge.

(7) Transfer upper aqueous phase to fresh 1.5 ml tube. Add two volumes of 100% ethanol at RT, vortex, and stand at RT for 2 minutes.

(8) Spin precipitate 5–10 minutes with bench centrifuge. Discard supernatant, then wash pellet with approximately 0.5 ml of 70% ethanol. Dry moderately, then resuspend with 50 μ l of *stock 50 TE 1 (8)*.

(9) Use 10 μ l of this extract for further analysis, e.g. digestion with a restriction enzyme and electrophoresis. If small DNA fragments are expected, add *stock boiled RNA'se A* (10 mg/ml, Boehringer) to give a final concentration of 20 μ g/ml, before or after restriction enzyme digestion. Removal of the RNA'se is unnecessary, unless the DNA concentration is to be estimated by spectrophotometry.

Large-scale alkaline lysis

Variations that allow different day/night work schedules are included in the protocol that follows.

(1) Inoculate 5 ml of *stock 13 medium* containing ampicillin (50 mg/l) with a single colony from an agar plate. Incubate at 37°C with vigorous shaking for 2–4 hours until cloudy, or overnight (starter culture).

(2) Inoculate 500 ml of *stock LB medium* containing ampicillin (50 mg/l) with 5 ml of the starter culture. Incubate during the day for 3–4 hours, until culture reaches an OD 600 of 0.8–1.0. Alternatively, inoculate the 500 ml in the evening and culture overnight. Note: amplification of plasmid copy number by chloramphenicol treatment was not used here; sufficient yields were obtained without it (c.f. Maniatus et al. 1982).

(3) Pellet cells by light centrifugation, e.g. 4,000 rpm, 4 minutes, in Sorvall GS-3 fixed-angle rotor, RT or cold.

(4) Discard supernatant and wash cells by resuspending with 100 ml of *stock 10 TE 1(8)*. Pellet cells again as in step 3, and discard supernatant.

(5) Resuspend cells thoroughly in 8 ml of *stock GET* solution with freshly added lysozyme (50 mM glucose, 10 mM Na₂EDTA, 25 mM Tris.HCl, pH 8.0, lysozyme 5 mg/ml). Use 10 ml pipette to assist resuspension, then transfer the cells to a 50 ml Nalgene polycarbonate tube, or other suitable tube.

(6) Add 16 ml of a freshly made solution of 0.2 M NaOH and 1% SDS, prepared from *stock 5M NaOH* and *stock 10% SDS*. Mix thoroughly but gently by inverting the tube two or three times, with parafilm cover. Stand tube on ice for 10 minutes.

(7) Add 12 ml of *stock 3M potassium, 5M acetate*. Mix by inverting the tube sharply several times, with parafilm cover. Stand tube on ice for 10 minutes.

(8) Centrifuge in either a Sorvall HB4 swing-out rotor, 9000 rpm (9,750 g), or a Sorvall SS34 fixed-angle rotor 10,000 rpm (10,400 g), 15 minutes, 4° G. The bacterial cell DNA and debris should form a tight pellet.

(9) Transfer supernatant to two 50 ml Nalgene tubes (approximately 18 ml to each). Add 0.6 volumes of isopropanol (12 ml) to each tube and mix well. Allow plasmid DNA to precipitate by standing tubes at RT for 15 minutes.

(10) Centrifuge in Sorvall SS34 rotor, 10,000 rpm, 30 minutes, at RT. Discard supernatant, then wash pellets with several ml of 70% ethanol. Dry moderately, and resuspend both pellets in a total of 8 ml *stock 10 TE 1(8)*. At this stage the pellets should have a translucent, colourless, rubbery appearance, and should dissolve readily.

Note: (1) to wash large (visible) DNA pellets it is not necessary to centrifuge them with the 70% ethanol, (2) plasmid DNA prepared in the manner above may be further purified by RNA^{se} treatment and phenol/chloroform extraction, or by centrifugation with caesium-chloride and ethidium bromide, as described next.

Purification of plasmid DNA by centrifugation with ethidium bromide in a caesium chloride density gradient

This method relies on the fact that ethidium bromide intercalates with double-stranded DNA in a way that depends on the conformation, supercoiled or relaxed, of the DNA. Plasmid DNA is circular and supercoiled when completely intact. The supercoiling reduces intercalation by ethidium bromide, so intact plasmid DNA retains a greater density than relaxed DNAs which bind more ethidium bromide (for example, nicked plasmid circles and linear fragments of nuclear, chromosomal DNA).

During centrifugation, caesium chloride (CsCl) solution forms a density gradient, and DNA molecules of different density migrate upwards or downwards to different positions according to the density of the surrounding gradient. The equilibrium position for each DNA molecule is where the density of the surrounding solution equals the density of the molecule, and the molecule migrates no further. Molecules of similar density are concentrated into one band. Centrifugation must be long enough for a gradient to form and for DNA molecules to reach their equilibrium positions. Excessive centrifugation compresses the gradient, and the DNA bands within it, towards the bottom of the tube. Only half the amount of ethidium bromide recommended by Maniatus et al. (1982) is required, a reduction that was found by trial to work and which is favoured because ethidium bromide is a potent carcinogen:

(1) Measure the volume of DNA solution (e.g. the dilute extract obtained by large-scale alkaline lysis) in a glass cylinder, and add 1 g CsCl for each millilitre. Cover with parafilm and mix gently by inversion. Stand cylinder for 1 hour, RT, to ensure that the CsCl dissolves completely. This solution may be stored at 4–8°C for at least a week, or may be frozen and stored indefinitely. CsCl will precipitate during storage, and larger protein aggregates may form. The latter may form immediately in any case, but are only an inconvenience (for loading through syringe, later). Protect the solution from light during storage.

(2) Add 0.4 ml of *stock ethidium bromide* solution (10 mg/ml in H₂O) for every 10

ml of CsCl solution. Mix well.

(3) Load the solution into a tube suitable for ultracentrifugation. For example, one 13.5 ml, polyallomer Beckman Quick-Seal tube will take the extract from one 500 ml cell culture that has been resuspended in 8 ml *stock 10 TE 1(8)* with 8 g CsCl and 0.32 ml *stock ethidium bromide* (10 mg/ml). A wide gauge disposable syringe fitted with a 10 ml barrel makes a convenient funnel. Pair tubes with DNA-CsCl-EthBr solutions of similar volume, or use CsCl blanks (1 mg CsCl/ml H₂O).

(4) Balance the paired tubes exactly with CsCl solution, and top with water-saturated paraffin oil. Check balance again, then seal.

(5) Centrifuge at 45,000 rpm for 36 hours, or 40,000 rpm for 40 hours, at 15°–20°C.

(6) Two bands may be visible in ordinary light, if the yield is high. Visualise faint bands with UV light. The upper band is linear bacterial DNA and/or nicked circular plasmid DNA. Insert a syringe into the top of the tube to let air in, then remove lower band with a second syringe. Lightly plug the upper syringe with tissue paper to prevent ethidium bromide solution squirting out. If only one band is found, take that. Record volume of the DNA fraction in the syringe (usually 1–2 ml), and transfer the fraction to a sterile glass tube.

(7) Add 1–2 volumes of water-saturated butanol, or pure isoamyl alcohol, cover tube, and shake to extract ethidium bromide. Repeat extraction four to six times, discarding the upper, non-aqueous phases.

(8) Place the lower, aqueous phase in a suitable ultracentrifuge tube, and dilute residual CsCl by adding *stock 10 TE 1(8)* (use 2x the original fraction volume). Beckman open-topped polyallomer tubes are suitable, 14 x 89 mm for SW41 Ti rotor, 25 x 89 mm for SW28 Ti rotor.

(9) To the new volume add two volumes of 100% ethanol. Mix well. If a large yield of DNA is expected, more than 50 µg for example, centrifuge immediately. For small yields, or if in doubt, stand tubes at -20°C for 1–2 hours. Some CsCl may precipitate, but will be removed by later steps. Centrifuge at 20,000 rpm, 1 hour, 4°C.

(10) Resuspend in 0.1–0.5 ml *stock 10 TE 1(8)*, depending on amount of DNA visible or expected, and the concentration desired. Use 10 µl diluted with 980 µl H₂O to estimate concentration by spectrophotometry (protocol 3, above). Check purity by agarose gel electrophoresis. There should be no high molecular weight bacterial DNA, and little low molecular weight RNA. Freshly extracted plasmids often form concatamers, resulting in more than one electrophoretic band. The extract is pure enough for most purposes, including restriction enzyme digestion and nick-translation.

10.2.5 DNA cleavage by digestion with restriction enzymes

Restriction enzymes (endonucleases) were obtained from Amersham, Bethesda Research Laboratories, Boehringer, New England Biolabs, and Pharmacia. Reaction mixtures for plant total-DNA were as follows: 2–8 µg DNA with 3–4 units of enzyme per µg DNA, in 20 to 50 µl of buffer comprised of DNA solution (DNA in 10 µl or less of *stock 10 TE 1(8)* or H₂O), 10x stock digestion buffer (10% of final total volume), and H₂O. Excess amounts of enzyme were added to allow for error in the estimations of DNA amount. To

establish many reaction mixtures at the same time, DNA was added to each tube in a fixed volume, plus or minus 2 μ l, and mixed with an appropriately sized aliquot from a single pot of fresh, pre-mixed restriction enzyme and buffer, held on ice. This ensured uniform application of enzyme to each DNA sample, and reduced the manual effort. 10x buffers used were the *stock high, medium, and low salt* buffers recommended by Maniatus et al. (1982), or the *stock Tris-acetate (TA) buffer* of O'Farrell et al. (1980). TA buffer was satisfactory for *Bam* HI, *Eco* RI, *Hinf* I, *Kpn* I, *Rsa* I, *Taq* I, and *Xba* I, the enzymes most frequently used here. Incubation times were generally 1–3 hours, at 65°C for *Taq* I and 37°C for the other enzymes. Double digestions at 37°C were performed by incubating two enzymes at the same time in TA buffer. For double digestions, *Taq* I was added second and incubated at 65°C, after initial digestion at 37°C with a different enzyme. All reactions required for electrophoresis were stopped by adding a one-tenth volume of *stock bromophenol blue (BPB) running dye* (final concentrations in reaction mix: 0.01% w/v BPB, 6.8% v/v glycerol, 45 mM Na EDTA). Stopped reaction mixtures were sometimes stored at 4°C or -20°C, and thawed at RT or 60°C, before electrophoresis.

10.2.6 Agarose gel electrophoresis

DNA fragments were electrophoresed in horizontal-slab agarose gels (Figure 10.13) of various agarose concentrations and physical dimensions, chosen according to the expected fragment sizes (kbp) and amount (μ g) DNA loaded. For rDNA analysis of total-DNA, gels were generally of 0.8–1.0% agarose, 13 cm wide, and 18 cm long from the loading slots. Reaction mixtures containing 4 μ g total-DNA were loaded into slots 7 mm wide and electrophoresed overnight for approximately 12 hours at 16 mA and 40 V (fixed voltage), in TAE buffer (40 mM Tris-acetate, 1 mM Na₂ EDTA) prepared from *stock 50x TAE*.

To stain the DNA for UV light photography, each gel was immersed in approximately 200 ml H₂O before adding 5 μ l of *stock ethidium bromide* (10 mg/ml H₂O). After gentle horizontal under a gentle flow of clean, cold tap water for 15–40 minutes, gels were illuminated from underneath with a 302 nm Transilluminator (UVP Inc.) and photographed in black and white with Polaroid positive/negative plates. DNA fragment sizes were determined by comparing their mobility with fragments of known size (size markers). Commercially supplied Lambda phage DNA (Boehringer) digested with *Hind* III was routinely used to provide markers. DNA fragments in total-DNA samples were only seen after Southern transfer from the gels and hybridisation probe analysis. Every gel was photographed immediately after electrophoresis to record the size markers, before Southern transfer, and also to record the success or otherwise of the restriction enzyme reactions.

10.2.7 Electroelution of DNA from agarose gels

Ribosomal DNA fragments were excised from recombinant plasmids with restriction enzymes, electrophoresed, visualised in UV light, and then electroeluted for sub-cloning (this chapter), restriction-site mapping (Chapter Twelve), and for preparing radioactive

DNA probes (Chapters 4–6). Two methods were used, essentially as described by Maniatus et al. (1982): electroelution from pieces of gel placed in a dialysis bag (Sartorius collodion bag), and electroelution into a trough cut in the gel immediately in front of the desired DNA band.

The eluted DNA fragments, in various volumes of electrophoresis buffer, were precipitated with two volumes of *stock ethanol and sodium acetate* solution, then centrifuged at high speed in Beckman SW28 or SW41 swing-out rotors, 20,000 rpm, for 1 hour, 4°C. To further remove gel contaminants, the fragments were resuspended in 0.2–0.4 ml stock *10 TE 1(8)* with addition of proteinase-K (final conc. 100 µg/ml) and SDS (final conc. 0.1%) and incubation at 37°C for 20 minutes. After one extraction with phenol and chloroform, the DNA was again precipitated, before final resuspension in *stock 10 TE 1(8)* to a convenient concentration (0.2–1.0 µg/ml), according to the expected yield, or the minimum volume needed for complete resuspension (50–100 µl).

10.2.8 Southern transfer

The following protocol, modified from Reed and Mann (1985) and Southern (1975), was used after electrophoresis to bind denatured (single-stranded) DNA to nylon filters.

(1) Place gel upside-down in a dry plastic box and submerge with *stock denaturing solution* (0.5 M NaOH, 0.5 NaCl). Cut away one corner for future orientation. Shake gently 30–60 minutes with horizontal motion.

(2) While the DNA denatures, cut and label a gel-sized piece of nylon filter (Gene Screen) with a ball-point pen, and cut away one corner for orientation. Soak the filter for at least 10 minutes in H₂O. Also prepare three gel-sized sheets of Whatman 3 mm chromatography paper. Soak one sheet in denaturing solution, drain excess liquid, and place the sheet on a flat plate. Later, this paper helps reduce lateral distortion of the gel.

(3) Place gel upside-down on the filter paper and blot excess liquid from the base plate. During electrophoresis, DNA migrates close to the underside, so DNA transfer upward is faster and more direct with this side of the gel upwards. The underside is also smoother, giving a better contact with the nylon filter, next.

(4) Lay wet nylon filter over the gel, orientating the cut corner with the cut corner of the gel. Line top edge along the leading side of the sample slots. Later, the edge of the filter provides a reference point for comparing migration of sample DNA fragments with the previously photographed DNA size markers.

(5) Briefly soak the second sheet of chromatography paper in H₂O and drain excess liquid. Place paper over the nylon filter, then use a Pasteur pipette to roll out air bubbles. Add the third sheet of chromatography paper, then stack 2–3 cm of paper hand towels on top. Cover with a flat plate and a centrally positioned weight of 200–500 g. Leave for at least 4 hours, or as much as 2 days if desired.

(6) Rinse the nylon filter for 1–5 minutes in 2x SSC at RT, blot lightly and place filter between two sheets of stapled blotting paper. Bake in tap-vacuum oven, 80°C, for at least 40 minutes and no more than 3 hours. Store at RT or cold, for up to at least 3 months if desired.

10.2.9 Preparation of radioactive probe by Nick-translation

Radioactive probes were made using a commercially prepared kit with convenient stocks of enzyme and non-radioactive nucleotide. Probes were usually made and used within a few days after arrival of fresh radioactive nucleotide. The following protocol (N. Contreras, pers. comm. 1986) is a modification of that recommended by the kit manufacturer (Bresa).

(1) To a 1.5 ml Eppendorf tube add the following in the order given: 0.5 ug DNA in 6 ul H₂O or *stock 10 TE 1(8)*, 4 ul buffer plus nucleotide cocktail (125 uM dATP, dGTP, and dTTP in 250 mM Tris.HCl, pH 7.6, 50 mM MgSO₄, 0.5 mM dithiothreitol and 250 ug/ml gelatin), 5 ul enzyme mix (5 units of *E. coli* DNA Polymerase I and 40 pg DNA'se I in a storage buffer of 40 mM potassium phosphate, pH 7.0, 1 mM MgCl, 0.2 mM DTT, 50% glycerol, and 200 ug/ml gelatin), 5 ul 2-³²P-dCTP (10 mCi/ml, specific activity 3000 Ci/mmol, Amersham). Vortex tube briefly, and spin for a few seconds in bench centrifuge.

(2) Incubate in 14°C water bath, 60 minutes.

(3) To remove unincorporated nucleotides, add 200 ul *stock 10 TE 1(8)* and apply the mixture to a Sephadex G-50 column, previously prepared in a disposable plastic column (Affini column, Amicon AF-100, diameter 8 mm, height 55 mm). Place column in 12 ml plastic tube (Falcon 2057) and centrifuge lightly in swing-out rotor, 3000 rpm (1,400 g), 3 minutes (Clements G-200 bench centrifuge). Discard column and store eluate at -20°C until required.

(4) Prepare hybridisation solution by mixing the radioactive probe with a maximum of 30 ml of fresh pre-hybridisation solution. This may be frozen stock thawed with a 50°–60°C water-bath, or new, and contains 0.1% SDS, 3x SSC, 5x Denhardt's solution, 50% formamide, 3 mM Tris.HCl; pH 8.0, and 0.3 mM Na₂EDTA prepared with 100% formamide (Fluka, highest purity) *stock 10% SDS, 20x SSC, 100x Denhardt's*, and *10 TE 1(8)*. Use minimum volume needed to just cover filter(s) in the hybridisation container.

During the nick-translation reaction, DNA'se I nicks the probe DNA, and DNA polymerase I catalyses incorporation of radioactive nucleotides into new DNA strands via the nicks (Old and Primrose 1981). The success of the reaction can be measured as the percentage incorporated radioactivity, (incorporated cpm/ total cpm) x 100. Incorporation (cpm) is measured by counting the number of radioactive emissions per minute from the probe DNA, after precipitation from an aliquot of the completed reaction mixture. Total cpm are measured directly from a second aliquot. The nick-translation protocol described above usually gives percentage incorporations of 30–60% (N. Contreras, pers. comm. 1988). Routine measurement of percentage incorporation was not needed because similar amounts of DNA were used in each reaction. Instead, the approximate incorporation (cpm) by the total eluted probe was routinely checked with a hand-held Geiger counter, for comparison with previous probes.

10.2.10 Hybridisation of radioactive DNA probe with DNA on a nylon filter

(1) Prehybridisation treatment: after Southern transfer (see above), soak filter in *stock pre-hybridisation solution* (0.1% SDS, 3x SSC, 5x Denhardt's solution, 50%

formamide, 3 mM Tris.HCl, pH 8.0, and 0.3 mM Na EDTA), 10 minutes –1 hour, 37°C, with gentle horizontal shaking. Fully immerse one or more filters individually in the pre-hybridisation solution, in a plastic food box covered to prevent evaporation. Just before the probe is ready to use, remove the filters and place them aside on the overturned lid. After use, store the pre-hybridisation solution at -20°C, and re-use several times (but do not use for mixing with probes). Thaw in water-bath, 50–60°C, until precipitates of SDS and protein dissolve, giving a clear or slightly opaque solution.

(2) Boil probe to produce single strands: place probe solution (usually 25–30 ml) in a 100 ml conical glass flask and incubate with water-bath 95°–100°C, for 3–6 minutes. The probe DNA is now ready for hybridising to complementary single-stranded DNA bound on the filter.

(3) Remove and immediately pour probe into the empty box used for pre-hybridisation. The probe temperature should not be allowed to drop below 37°C, since this could promote a significant amount of reannealing by the probe (to the double-stranded state).

(4) Hybridisation: place up to three filters in the probe solution. Immerse one end of a single filter, then lower the rest of the filter carefully to prevent air bubbles being trapped. Before and after each filter, tilt the box to ensure complete coverage with probe. Cover box, and incubate at 37°C for at least 4 hours and as much as 18 hours, with gentle horizontal shaking. After hybridisation, return probe to the 100 ml conical glass flask, and store at 4°C or -20°C for reuse.

(5) To remove unbound or weakly bound probe, wash filters four times with a solution of 2x SSC, 0.1% SDS, pre-heated to 65°C, 10–15 minutes per wash, with gentle horizontal shaking. Cooling of the wash solution can be reduced by using a large volume (e.g. 250 ml per wash), which also lets the filters float separately. The number of washes seems to be more important than the time given to each. Filters can be left in the final wash solution at RT for at least a few hours, if desired, before autoradiography.

After the filter is washed, all DNA bound by Southern transfer remains, together with any probe DNA that has formed sufficiently strong complexes with similar or identical sequences on the filter. Low stringency washes separate only very weak complexes, and high stringency washes separate very strong complexes. The strength of each complex reflects the degree of sequence similarity between the probe and the target DNA. The stringency of the wash can be increased by decreasing SSC concentration, increasing formamide concentration, or by increasing the treatment temperature. The choice of conditions depends on the expected similarities between probe and target DNA fragments, and the desired sensitivity of detection.

The washing protocol given above was suggested by R. Appels (pers. comm. 1986) on the basis of work with wheat rDNA probes, and was routinely used here for taro rDNA probes hybridised with DNA from taro and its near relatives. Different conditions were used in preliminary experiments with chloroplast, mitochondrial, and rDNA probes from distantly related plant taxa (Chapter Eleven).

10.2.11 Reuse of probes and filters

Probes can be used a few times depending on the number of filters probed each time and the amount of probe removed by each filter. When severe non-specific binding occurs (artefactual spots and general smears), a large proportion of the probe may be lost (test probe solution with Geiger counter). A probe made with high incorporation of ^{32}P can be reused for at least two weeks, but will lose most radioactivity within a month because the half-life of ^{32}P is two weeks. Filters were cleaned for reuse by removing probe DNA with high stringency washes:

(1) Keep filter moist with water. It is more difficult to remove probe from dry filters.

(2) Probe stripping. Method 1 — wash filter 3 times with at least 200 ml H_2O , 85–95°C, 5 minutes each time, with horizontal motion shaking. Method 2 — wash filter once with hot water, as above, then wash for 10 minutes in 25 mM NaOH at RT. Wash twice more with hot water. Blot and store at RT or 4°C if desired.

(3) Treat as for a fresh filter.

10.2.12 Autoradiography

(1) After washing, blot radioactive filter lightly and seal within a very thin plastic bag.

(2) Place detector of a Geiger counter on the filter to locate and measure radioactive DNA bands. Choose an initial exposure time accordingly (30–60 minutes for bands emitting more than 500 cpm, 6 hours for emission of 50 cpm, 12 hours for emission of 10–20 cpm, 1–3 days if there is no clear signal).

(3) In a darkroom, sandwich the filter between two sheet of X-ray film (Fuji, NIF RX Medical), between two intensifying screens (Kodak) in a metal cassette: tape the filter and lower X-ray film to the lower intensifying screen, to prevent movement when the upper X-ray film is removed later. Mark both X-ray films to record the upper corners of the filter; these corners define the electrophoretic starting line. The exact position of the filter often becomes visible later, after development, as an outline against the area outside the filter.

(4) For short exposure, less than one hour, store the cassette at RT. For longer exposure, store cassette at -70°C. This gives sharper bands than long exposure at RT. Expose the upper sheet no longer than is thought necessary for the most radioactive bands on the filter. Replace the top sheet with a fresh sheet of film, develop the first film, and use this to guide exposure of the fresh film just added. Allow the lower film to over-expose with respect to the strongest bands, so that weak and possibly unexpected bands become visible.

10.2.13 Molecular cloning of taro rDNA

Taro *Eco* RI fragments were ligated into the tetracycline resistance gene of pBR322 and the ligation mixture used to transform *E. coli* strain RR1. Transformed bacteria, with ampicillin resistance conferred by pBR322, were immediately selected for by culturing the transformation mixture on agar plates with ampicillin. Transformants were replica-

plated directly onto agar plates with ampicillin, for maintenance, and onto nitrocellulose filters on ampicillin plates for further screening essentially as described by Grunstein and Hogness (1975). Six hundred transformant colonies were screened, and four were found with recombinant plasmids containing taro rDNA. The steps are described in detail below:

DNA preparation

Ribosomal DNA was partially purified by centrifuging total DNA to equilibrium in a CsCl/actinomycin-D density gradient, essentially as described by Gerlach and Bedrook (1979). *Eco* RI fragments were then prepared for cloning.

High molecular weight total-DNA was extracted from *C. esculenta* var AKL 34 using the protocol described above. The extract was quite pure (OD 260/280 = 2.0), with some RNA. Approximately 800 ug DNA was dialysed overnight against 25 mM sodium tetraborate, pH 9.0, giving a final volume of 2 ml. CsCl (58.07 g) was dissolved in 25 mM sodium tetraborate, pH 9.0, in a volume of 65 ml. The DNA solution and 400 ul actinomycin-D (0.5 mg/ml in 25 mM tetraborate, pH 9.0) were added, with further tetraborate solution to give a final volume of 68 ml (CsCl density 0.85 g/ml, weight actinomycin D/ weight DNA ratio 1: 4).

The solution was split between two polyallomer centrifuge tubes (Beckman Quick Seal), and centrifuged for 60 hours at 45,000 rpm. This produced a gradient with a clearly visible yellow band of actinomycin-D complexed with DNA, halfway down the tube. Fractions of 1 ml were taken from the bottom, and their OD 260 values determined (Figure 10.14).

Actinomycin-D binds to external guanosine residues on DNA double helices, forming complexes of lower density than DNA alone. Because rDNA repeats are relatively rich in guanosine, compared to most DNA in the extract, rDNA binds more actinomycin-D and reaches an equilibrium position of relatively low density. Aliquots (20 ul) from several fractions were tested for rDNA by dot blotting to a filter and hybridisation with a wheat rDNA probe, as follows. To each aliquot, 50 ul of *stock denaturing solution* (0.5 M NaOH, 0.5 M NaCl) was added. The mixture was incubated on ice for 5 minutes before adding 200 ul of ice-cold *stock neutralising solution* (3 M NaCl, 0.5 M Tris.HCl). After further incubation on ice (5–10 minutes), the mixtures were suctioned through a nylon filter, pre-soaked with H₂O and held in a perspex dot-blotting device with circular wells and attached to a tap-vacuum. The mixtures were suctioned through a nylon filter. Each well was rinsed with a further 100 ul of *stock neutralising solution*, before baking the filter in a vacuum oven.

Using the standard protocols for hybridisation probe analysis (see above) the filter was probed with pTA250.2, which contains a wheat rDNA fragment spanning the 18S–26S genic region (courtesy R. Appels). After washing with 2x SSC and 0.1% SDS at 65°C, three peak rDNA fractions were detected (Figure 10.14), and pooled.

DNA from the pooled fractions was recovered by precipitation with 2 volumes of isopropanol saturated with NaCl, and centrifugation overnight in a swing-out rotor (20,000 rpm, Beckman SW 27). The precipitate was resuspended in 450 ul *stock 10 TE*

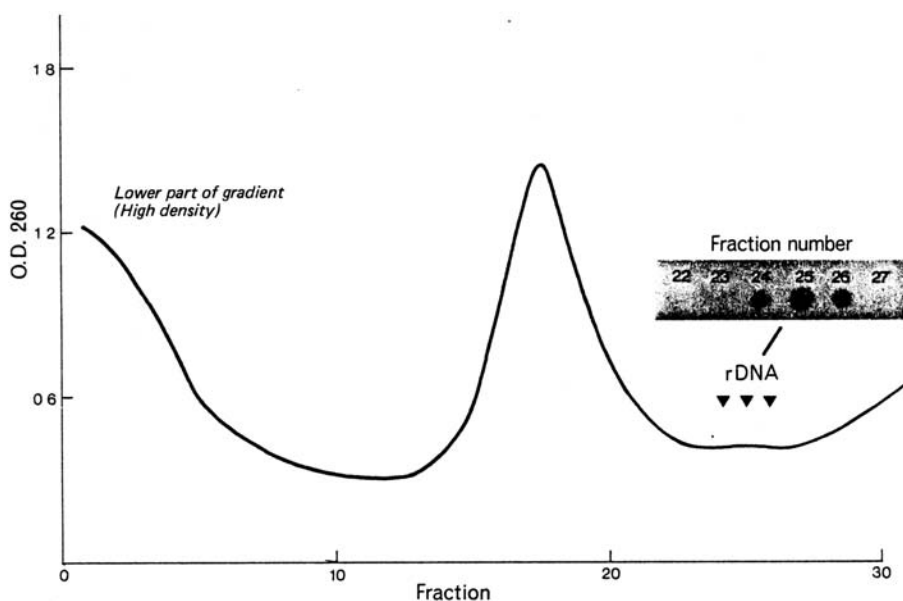


Figure 10.14 Partial purification of ribosomal DNA (enrichment procedure). After centrifuging total-DNA from AKL 34 to equilibrium, in a caesium chloride and ethidium bromide density gradient, 1 ml fractions were removed from the bottom of the tube, and aliquots diluted for optical density analysis at 260 nm. Aliquots (20 μ l) from lower density fractions above the DNA peak were transferred to a nylon filter and hybridised with a cloned wheat rDNA fragment (pTA250.2) to determine the peak rDNA fractions (24–26, inset).

1(8), and incubated with 0.1% SDS (4.5 μ l *stock 10% SDS*) and 20 μ g proteinase K (20 μ l fresh solution, 1 mg/ml H_2O , at 37°C, 10 minutes). After one extraction with phenol and chloroform, the DNA was precipitated with ethanol and sodium acetate, and resuspended in 100 μ l *stock 10 TE 1(8)*.

Preliminary experiments (see Chapter Eleven) established that taro rDNA possesses two *Eco* RI restriction sites. To create fragments suitable for cloning, 80 μ l of the rDNA enriched extract was digested with approximately 30 units of *Eco* RI in a reaction volume of 100 μ l (37°C, 1 hour, with appropriate buffer). After adding 30 μ l of 5% SDS and incubating at 65°C for termination, the DNA fragments were stored at -20°C. The rDNA of *Eco* RI restriction fragments were subsequently fractionated by differential velocity centrifugation in a glycerol gradient (protocol of R. Appels, pers. comm. 1986), as follows:

The preliminary experiments showed that the *Eco* RI fragments lay within the 2–10 kbp size range, and to isolate fragments in this range, the *Eco* RI reaction mixture was thawed at 65°C, to dissolve SDS, and loaded onto a linear gradient of 10–40% glycerol. The gradient was prepared in a 13.2 ml polyallomer tube, then was allowed to stand 4 hours at 8°C to stabilise, before the DNA fragments were added. Centrifugation in a

swing-out rotor (Beckman SW 41, 27,000 rpm, 22 hours, 5°C) was terminated without braking after reducing speed to 2,000 rpm. Three fractions — the lower, middle, and upper thirds of the gradient — were taken from the bottom, and the DNA in each was precipitated with ethanol and sodium acetate.

Each fraction was processed further and the contents examined by electrophoresis, Southern transfer, and hybridisation with pTA250.2, to confirm the distribution of large and small *Eco* RI taro rDNA fragments. The desired fragments were expected in the middle fraction (2–10 kbp size range), and the following steps apply to this fraction. After centrifugation in a swing-out rotor (Beckman SW 27), 25,000 rpm, 3 hours, the precipitate was resuspended in 400 ul *stock 10 TE 1(8)*. This was incubated with SDS and proteinase K as previously, and extracted once with phenol and chloroform, with a further 50 ul of *stock 10 TE 1(8)* used to back-extract residual DNA from the phenol/chloroform phase. The fragments were again precipitated with ethanol and sodium acetate, spun for 20 minutes in a bench centrifuge, and washed with 70% ethanol, with a further 15 minutes of centrifugation. The precipitate was finally resuspended in 50 ul H₂O, ready for cloning.

Ligation to pBR322

An unknown but small weight (less than 1 ug) of *Eco* RI fragments in 1, 5, or 10 ul of the final suspension (above) was placed in a 1.5 ml Eppendorf tube on ice, with addition of H₂O to a volume of 10 ul (if not already this volume), before mixing with 3 ul of commercially supplied pBR322 previously cut with *Eco* RI and dephosphorylated (0.1 ug/ul, BRL), 6.5 ul of ligation reaction mixture (fresh *stock solution* containing 8 parts *stock 5x ligase buffer*, 4 parts 10 mM ATP, and 1 part 1 M dithiothreitol), and 0.5 ul T4 DNA ligase (400 units/ul, BRL). This reaction mixture (final volume 20 ul) was incubated 4–20 hours at 14°C. The mixture was stored at -20°C without further treatment prior to transformation of competent cells.

Preparation of competent cells and transformation with the ligation products

One ml of overnight culture of *Escherichia coli*, strain RR1, was placed in 100 ml of fresh *stock LB medium* and incubated at 37°C with vigorous shaking until an OD 600 of approximately 0.7 was reached. Four 10 ml aliquots of cells were transferred to sterile plastic centrifuge tubes and centrifuged at 2000 rpm for 5 minutes. The supernatants were discarded, and the cells then resuspended in 5 ml cold MgCl₂ (0.01 M, approximately 5°C) per tube, and centrifuged (2000 rpm, 5 minutes). The supernatants were discarded. Each pellet of cells was resuspended in 5 ml cold CaCl₂ (0.05 M, approximately 5°C). The cells were resuspended and pooled in a total of 2.5 ml cold CaCl₂ (0.05 M, approximately 5°C). These cells, now competent for the uptake of plasmids, were held on ice for immediate transformation or stored for a few days at -20°C.

For transformation, 100 ul of competent cells were mixed with 38 ul cold CaCl₂ (0.05 M) and 2 ul of ligation mixture (containing 30 ng of the vector, pBR322). This was incubated on ice for 1 hour, then at 42°C for 2–3 minutes (heat shock). *Stock LB*

medium, 0.5 ml at RT, was added and the cells were incubated at 37°C for 1 hour, with shaking. The culturing step gives any plasmids that have entered cells an opportunity to replicate and express their antibiotic resistance genes. Three ml of top-agar (LB medium with agar, 45°C) was added to the final transformation mixture and poured onto one fresh LB agar plate (*stock LB medium* with 15 g Bacto-agar/l) with ampicillin (50 mg/l). After letting the top-agar set, the plate was inverted and incubated at 37°C overnight (Figure 10.15A).

RR1 is a fast-growing strain of *E. coli*, and embedding with top-agar constricted growth so that most colonies remained discrete. With a toothpick, individual colonies were transferred to a second ampicillin plate (Figure 10.15B) according to a paper grid sheet placed beneath the plate (100 colonies per plate). After overnight culture at 37°C, a brass stamp with 100 protrusions was used to replicate the colonies onto two ampicillin plates successively: first onto a nitrocellulose filter disk (Schleicher and Schuell, 82 mm diameter, 0.45 µm pores) previously laid on one plate, and then directly onto the agar of a second ampicillin plate. Between different sets of colonies, the brass stamp was washed in ethanol and flamed with a Bunsen burner. Both plates were cultured overnight at 37°C (Figure 10.15C). After culturing, the second plate was stored at 4°C until further required. The filter was transferred to an agar plate (LB medium) with chloramphenicol (30 mg/l) and incubated at 37°C overnight, 14–16 hours (Figure 10.15D). This antibiotic inhibits cell division, but allows replication of the plasmid DNA, increasing the yield of plasmid DNA for each colony.

Screening colonies for plasmids with DNA inserts

Six hundred transformant colonies were obtained and cultured on six nitrocellulose filters. After chloramphenicol treatment (above) each filter was placed on a disk of Whatman No. 1 paper saturated to brimming with 3.5 ml of *stock denaturant* (0.5 M NaOH, 0.5 M NaCl), for 10–15 minutes (Figure 10.15E). This treatment lysed the cells and denatured the DNA simultaneously. After lysis, the filter was placed on blotting paper to remove excess denaturant, and then placed on a disk of No. 1 Whatman paper saturated with 3.5 ml *stock neutralising solution* (3 M NaCl, 0.5 M Tris.HCl), for 10–15 minutes (Figure 10.15F). The filter was laid on blotting paper to remove excess neutraliser, then put between two loose sheets of blotting paper for baking in a tap-vacuum oven (80°C). Several filters were placed in one 500 ml, deep glass beaker and incubated with pre hybridisation and hybridisation solutions as described above for Southern transfer filters. To detect plasmids containing rDNA inserts, wheat rDNA excised from pTA250.2 and electroeluted from agarose was used as a probe (Figure 10.16). Mini-scale plasmid DNA preparations of all apparently positive colonies were prepared and digested with *Eco* RI, then electrophoresed and transferred to filters by Southern transfer for hybridisation probe analysis, again with the rDNA fragment from pTA250.2. Three rDNA clones were detected. False positive colonies found in the initial colony screening were attributed to residual contamination of the probe rDNA fragments with pTA250.2 vector sequences, homologous to the vector used for cloning taro DNA (pBR322), or contamination with residual *E. coli* DNA. A fourth rDNA clone was

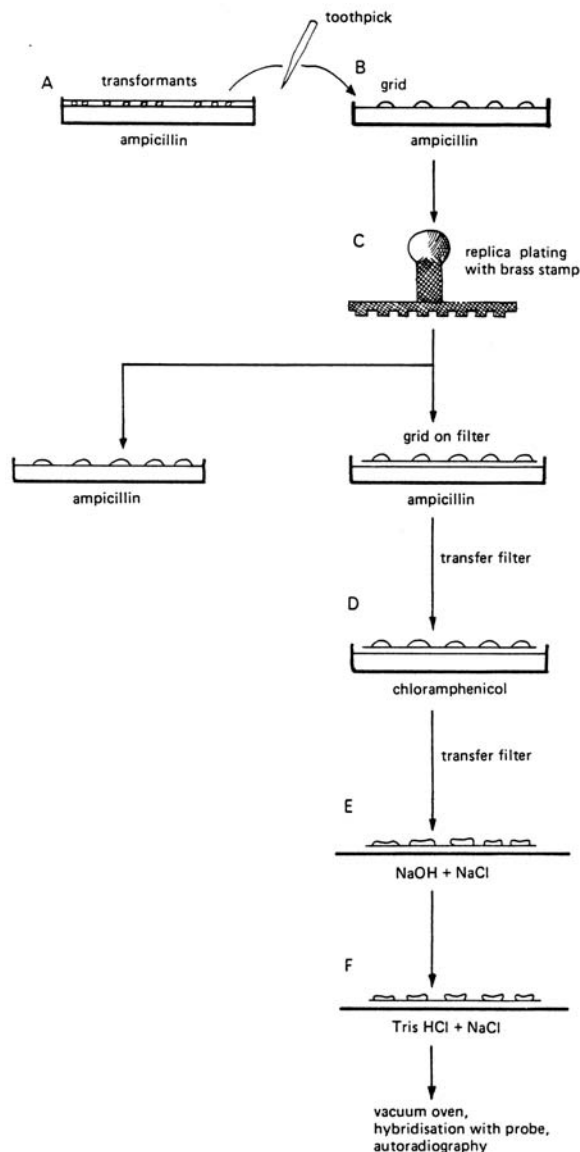


Figure 10.15 Screening for transformed cells and detecting recombinant clones by colony hybridisation, using the Grunstein Hogness method. See text for details. (A) Transformed cells of *E. coli* strain RR1 were selectively cultured in top agar on a medium containing the antibiotic ampicillin, for which the transforming plasmid pBR322 provides resistance. (B) Individual colonies were transferred by hand to a second agar plate according to a grid pattern, and then (C) replica plated with a brass stamp. One replica set of colonies was cultured then stored at low temperature, and a second was cultured on a nitrocellulose filter. (D) The filter was transferred to an agar plate with chloramphenicol, an antibiotic which stops bacterial cell growth but not the replication of plasmids in each cell. (E) To lyse the cells, the filter was transferred to blotting paper soaked with a strongly basic solution. After (F), treatment with a pH neutralising solution, (F) the filter was baked to help bind the released DNA, hybridised with a ^{32}P labelled rDNA probe, and autoradiographed (see Figure 10.16 for example).

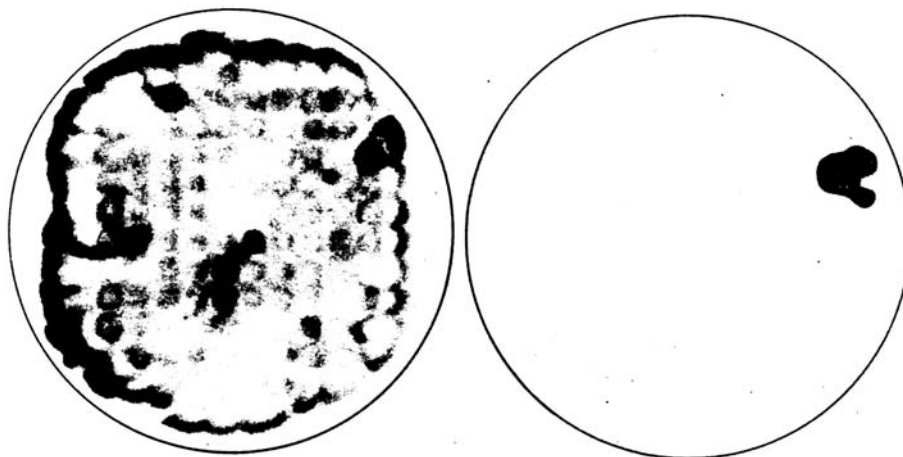


Figure 10.16 Colony hybridisation. A wheat rDNA insert purified from recombinant plasmid pTA250.2 was used to probe colonies of *E. coli* previously transformed with a ligation mixture of pBR322 and taro rDNA fragments (autoradiograph at left). The colonies were prepared on a filter as shown in Figure 10.15. Strongly hybridising colonies were analysed further after propagation from the stored replica date, plasmid extraction, agarose gel electrophoresis, Southern transfer, and hybridisation probe analysis with wheat rDNA from pTA250.2. Ribosomal DNA was detected only for the colony giving the strongest signal, upper right in the autoradiograph at left. The corresponding colony from the stored replica plate provided the recombinant plasmid pCe34.1. The taro rDNA insert from pCe34.1 was used to probe the filter again. Only the source colony for pCe34.1 contained DNA homologous to pCe34.1 (autoradiograph at right).

discovered when the original colony-blot filters were reprobbed with the taro rDNA fragment excised from pCe34.1 (5.5 kbp *Eco* RI fragment), and pCe34.2 (4.0 kbp *Eco* RI fragment).

Subcloning to provide a probe specific for variable region of the rDNA large intergenic spacer

A 2.8 kbp *Taq* I fragment was subcloned from pCe34.1 as follows. After purifying a large-scale preparation of pCe34.1 by equilibrium density centrifugation, in caesium chloride and ethidium bromide, plasmid DNA was digested with *Taq* I, electrophoresed, and the 2.8 kbp fragments electroeluted. After extracting proteins with phenol and chloroform, and precipitation with *stock ethanol and sodium acetate solution*, the *Taq* I fragments were resuspended to a concentration of 0.2 ug/ul in *stock 10 TE 1(8)*.

Linearised vector molecules, with sticky ends suitable for ligation with *Taq* I fragments, were prepared by digesting pBR322 (Boehringer) with *Cla* I. After cleaning with phenol and chloroform, and ethanol precipitation, the vector molecules were de-phosphorylated essentially as described by Maniatus et al. (1982). Approximately 5 ug pBR322 precipitate was resuspended in 44.5 ul H₂O, then mixed with 5 ul *stock Wx CIP buffer* (0.5 M Tris.HCl pH 9.0, 10 mM MgCl₂, 1 mM ZnCl₂) and 0.5 ul Calf

Intestine Phosphatase (9.5 units; Boehringer). This mixture (50 ul total) was incubated at 37°C for 30 minutes, before adding 0.5 ul *stock 10% SDS* and incubating at 68°C for 45 minutes. After extracting proteins with phenol and chloroform, the vector molecules were precipitated with ethanol and sodium acetate.

For ligation, 0.2 ug of vector in 2 ul *stock 10 IE 1(8)*, and 0.4 ug of *Taq I* rDNA fragments in 2 ul *stock 10 TE 1(8)* were mixed with 10 ul H₂O, 4 ul *stock 5x ligase buffer*, 2 ul 10 mM ATP, 0.2 ul 1 M dithiothreitol, and 1 ul (40 units) of T4 DNA ligase (New England Biolabs). After incubation overnight at 16°C, the mixture was stored at -20°C prior to transformation of *E. coli* strain RR1, essentially as already described. Fifty-four transformants were obtained.

Since ligation involved only one rDNA fragment, there was a good chance that the desired fragment would be found in a small sample of transformants. For initial screening, 47 colonies were transferred to one LB agar plate with ampicillin (50 mg/ml) and one LB agar plate with tetracycline (16 mg/l), using the same grid for each plate. The *Cla I* site is in the tetracycline resistance gene in pBR322, and insertional deactivation of the tetracycline resistance gene was indicated by fourteen colonies which grew very slowly or not at all in the presence of tetracycline. Transformant colonies from the ampicillin plate were grown and lysed on a nitrocellulose filter, essentially as described for the initial cloning procedure (above), and the filter was probed with the *Eco RI* fragment from pCe34.1. All 14 tetracycline sensitive colonies contained the 2.8 kbp rDNA *Taq I* fragment. One was chosen and named pCe34.11.

10.2.14 *In situ* hybridisation of rDNA to chromosomal loci

In situ analysis using three different tritium labelled nucleotides gives probes of high specific activity, and autoradiographic exposures of such great resolution that hybridisation within a chromosome can be detected. The high resolution results from radioactive emissions of low penetrating power (beta particles), and detection requires the intensity provided by high specific activity.

Chromosome preparation

Procedure courtesy L. McIntyre (pers. comm. 1987). The tips from several young roots were harvested (0.5 cm removed from roots 0.5–4 cm long) and placed in water on ice, overnight, or were *immersed with stock colchicine solution* (0.4% w/v in H90) for 2 hours at RT. These alternative treatments both serve to arrest cell division. Tips were fixed in a glass vial with a solution of ethanol and acetic acid (3:1) for between 4 and 24 hours. To soften the tissues, the fix solution was replaced with 1 M HCl and the tips incubated at 60°C, 4 minutes. The terminal 1–2 mm were removed and then placed in a drop of 45% acetic acid on a very clean, dust-free slide, near one end of the slide (for later dipping treatments). A cylindrical brass rod with a flat end of approximately 2 mm diameter was used to gently squash the meristematic cell region out of the root cap, and then to macerate the meristematic cells. Visible clumps of cells and root-cap epidermal tissue, were removed with tweezers and a cover slide placed over the preparation. A piece of blotting paper was placed over the slide, and with heavy thumb pressure the

cells were squashed. After checking for the presence of metaphase chromosome spreads, with a light microscope, the slide was frozen by dipping in liquid nitrogen, and the coverslip flipped off with a razor blade. The slide was dipped in 100% ethanol, next in 70% ethanol, and was then air dried at RT.

Synthesis of ³H copy-RNA probe from cloned rDNA

Procedure courtesy N. Contreras (pers. comm. 1987), modified from Pardue and Gall (1969). In an Eppendorf tube, 100 ul each of ³H-CTP ([5-³H] cytidine 5'-triphosphate, 28 Ci/mM, Amersham), ³H-UTP ([5,6-³H] uridine 5'-triphosphate, 32 Ci/mM, Amersham) and ³H-ATP ([2,8-³H] adenosine 5'-triphosphate, 41 Ci/mM, Amersham) were mixed and then dried in a rotary vacuum (Speedvac). The nucleotides were suspended in 15 ul *stock 10 TE 1(8)* (water is an alternative), with incubation at 37°C for 20 minutes to ensure complete suspension. Next, 0.2 ug of purified and proteinase K treated taro rDNA (insert from pCe34.1) was added in 10 ul H₂O, together with 10 ul of non-radioactive nucleotide, GTP (guanosine 5'-triphosphate, P-L Biochem). To this mixture were added 10 ul of *stock 5x RNA polymerase buffer* (40 mM Tris.HCl, pH 7.9, 10 mM MgCl, 0.1 mM Na₂DTA, 150 mM KCl, 500 ug/ml bovine serum albumin), 0.5 ul of 1 M dithiothreitol, and 5 ul ϕ . coll RNA polymerase (1 unit/ul, Boehringer) (50.5 ul final reaction volume). The RNA polymerase reaction was allowed to proceed for 30 minutes at 37°C, before removing 1 ul for estimating radioactive nucleotide incorporation. To remove DNA, 250 ul 0.05 M Tris, 10 ul DNA'se (0.2 mg/ml, Boehringer), 5 ul yeast RNA (10 mg/ml) and 5 ul CaCl₂ (0.01 M) were added and the mixture incubated a further 30 minutes at RT. The reaction was terminated fully by adding 25 ul Na₂DTA (0.25 M), 1 ul 5% SDS, 100 ul *stock phenol* and 100 ul *stock chloroform*. The phenol/chloroform phase was washed with 200 ul of 0.05 M Tris and the pooled aqueous phases were precipitated with 2 volumes of 100% ethanol. For final storage at -20 C, prior to in situ hybridisation, the precipitate was resuspended in 200 ul of 6x SSC, giving approximately 35,050 cpm/ul (incorporated radioactivity).

Estimation of percentage incorporation

After incubation, 1 ul of the RNA polymerase reaction mixture was removed, as noted above, and added to 99 ul of H₂O. Ten microlitres of the dilution were spotted directly onto a glass fibre filter (Whatman) for estimation of total radioactivity. A further 10 ul was mixed with 50 ul of sonicated salmon sperm DNA (2 mg/ml) and 1 ml of 5% (w/v) trichloroacetic acid. The mixture was placed on ice for 5 minutes to allow precipitation, before being loaded onto a second glass fibre filter. The filter was washed twice with 2 ml aliquots of 0.1 M Na₂H₂P₂O₇ (Sigma) in 1 M HCl, and then with approximately 10 ml of 100% ethanol. This filter was used to measure incorporated radioactivity. Two replica filters were prepared for measuring total and incorporated radioactivity, four filters in all. The filters were dried and placed in glass scintillation vials with scintillant (0.06% 2,5-diphenyloxazole, Calbiochem, and 0.006% 1,4-di (2-[5-phenyloxazolyl]-benzene, Calbiochem, in toluene). Radioactivity was measured with an automated scintillation spectrometer, and the percentage of radioactive nucleotides incorporated into

copy-RNA was calculated to be 4.2%, corresponding to 7,010,000 cpm from the full reaction volume.

***In situ* hybridisation**

Chromosome preparations (see above) were used for *in situ* hybridisation as described by Appels et al. (1978) with modifications recommended by N. Contreras (pers. comm. 1988). Several slides were processed at the same time, placed in Coplin jars for immersion. One hundred ml of 2x SSC was mixed with 0.1 ml pancreatic RNA'se A (2 mg/ml, final concentration 2 ug/ml, Boehringer) and preheated to 37°C. The slides were added and the jar incubated in a water bath for 30 minutes at 37°C. The solution was replaced with H₂O (37°C) to rinse the slides. To denature the DNA, the slides were incubated with 0.2 M HCl at 37°C for 10 minutes, then washed with H₂O three times, once with 70% ethanol, once with 95% ethanol, and then air dried in a rack. The tritiated copy-RNA solution (6x SSC) was mixed with an equal volume of formamide (Fluka) to give a hybridisation solution containing 3x SSC and 50% formamide. The amount of mixture prepared was enough to give each slide approximately 5 ul, placed centrally in the area with chromosomes (exact amount just enough to fill the area beneath the coverslip). Approximately 90,000 cpm of incorporated radioactive nucleotide was received by each slide, the recommended amount being 100,000 cpm (N. Contreras, pers. comm.) or 70,000–700,000 (Arnold 1985: 46). An acid-washed coverslip was removed from storage in 95% ethanol and placed on each slide, then sealed with rubber cement (bicycle glue) which was allowed to partially set. The slides were placed in a 60°C air incubator for 2 minutes, to ensure that the probe remained single-stranded for hybridisation, and were then placed in an air incubator at 37°C overnight (20 hours). Before the extended incubation, each slide was checked for possible leaks and sealed with further glue if necessary. Incubation at 37°C for 4 hours is sufficient, and the temperature can be adjusted according to the expected similarity of the probe and target sequences (identical in the present example).

After hybridisation, glue was removed with tweezers, and the slides were placed in a Coplin jar containing 3x SSC and 50% formamide at 37°C, and incubated for 5 minutes, allowing the cover slips to float off the removal. The slides were incubated for two further periods of 10–15 minutes with fresh solutions of 3x SSC, 50% formamide, at 37°C, and were then incubated for three periods of 10 minutes with fresh solutions of 2x SSC, RT.

To completely remove unannealed copy-RNA sequences, the slides were incubated in a solution of pancreatic RNA'se A (Boehringer, 2 ug/ml in 2x SSC) for 30 minutes at RT. They were then rinsed with six periods of 10 minutes in fresh solutions of 2x SSC and 0.1% SDS, at RT, two periods of 15 minutes in 70% ethanol, and two periods of 15 minutes in 95% ethanol. The slides were air dried at RT.

To prepare slides for autoradiographic exposure, all operations were conducted in a dark room equipped with a light brown safe light (Ilford No. 902). Silver emulsion (Ilford Nuclear Research Emulsion, particle size K2, stored cold in a lead container and wrapped in aluminium foil) was prepared by incubating Ilford K2 paste at 45–50°C until liquified,

then mixing with an equal volume of preheated H₂O (45–50°C). Slides were placed back to back, with the chromosome preparations downwards, and dipped half-way into the emulsion, taking care not to touch the sides of the container. Excess emulsion was drained by tapping the slides on blotting paper, before standing them separately and vertically, emulsion upwards, in an open rack. The slides were transferred to a slide box and air dried for 1–2 days at RT, in darkness. The box was then sealed with black tape, wrapped in at least two layers of aluminium foil, and stored at 4°C. Slides to be used for an initial test exposure of 5 days were stored in a separate box. Successful exposures were obtained after 2 weeks.

For autoradiographic development, all materials were first brought to RT. The slides were developed for two minutes in fresh Kodak Dektol solution (1:1 dilution with H₂O, no more than six weeks old) and fixed for 4 minutes with Kodak fixative. After rinsing in H₂O, the slides were allowed to dry before staining in Giemsa solution (5 ml Giemsa mixed with 2 ml of 1 M NaHPO₄/KH₂PO₄ buffer, pH 6.8, and made up to 100 ml with H₂O) for 8 minutes at RT. The slides were rinsed in tap water, and while still wet were viewed under a light microscope to determine the extent of Giemsa staining. If de-staining was required, the slides were dipped in 100% ethanol then washed again with water. After satisfactory staining, the slides were dried and then made permanent with Depex mounting medium, using large rectangular coverslips so that the entire area of the chromosome preparation could be viewed. Photomicrographs were taken with a Zeiss light microscope and Kodak technical pan film (2415).

10.2.15 Thermal melting point analysis

The one-step protocol described here is similar to that described by Gill and Appels (1988), with minor modifications. ³²P labelled probes, made with the taro rDNA insert from pCe34.1, were incubated with Southern transfer filters in the usual manner, in 3x SSC, 50% formamide, 0.1% SDS, 5x Denhardt's, 3 mM Tris.HCl, pH 8.0, 0.3 mM Na₂EDTA, at 37°C, 4–18 hours, as described above. After the usual low-stringency washes in 2x SSC, 0.1% SDS, at 65°C, autoradiographs were made without allowing the filters to dry. The thermal melting step that follows (high-stringency hybridisation) was sufficient to remove 50% of the probe hybridised to internal control samples of identical DNA. Each filter was placed in a thick, clear plastic bag, double-sealed at three sides before adding approximately 25 ml of a simplified hybridising solution (3x SSC, 50% formamide), at RT, and enough to easily cover the filter. Air bubbles were squeezed out, and the bag was closed by double-sealing. A water-bath was preheated to the desired treatment temperature (e.g. 66°C), and the bag was incubated for 15 minutes with occasional turning and squeezing so that all parts of the filter received equal treatment. The filter was removed, washed under low-stringency conditions (2x SSC, 0.1% SDS, 65°C), blotted to remove excess fluid, and was autoradiographed.

10.2.16 Mitotic-cell chromosome counts from root tips

The protocol of Matthews (1984) was used (see Appendix 10.1).

Chapter Eleven

Preliminary Trials of Methods for Analysing Variation

11.1 Introduction

The study of taro began with trials of a range of different methods for detecting genotypic variation. Variable and invariant isoenzymes were detected by electrophoresis of crude leaf-protein extracts, followed by biochemical assays of the electrophoresed proteins. The study of isoenzymes was abandoned because it seemed logistically and interpretatively more difficult than investigating DNA variation. Attempts to prepare pure chloroplast DNA were unsuccessful because starch grains in the chloroplasts disrupted chloroplast membranes during centrifugation, and for other reasons not determined. To obtain pure chloroplast DNA, improvements are needed in the prior growing conditions and in the protocol for purifying chloroplasts. The initial results of isoenzyme analysis and chloroplast DNA purification are not presented.

To quickly obtain information about chloroplast, mitochondrial, and ribosomal DNAs, extracts of total DNA from taro were digested with restriction enzymes, electrophoresed, transferred to nylon filters, and probed with pre-existing clones of DNA from plant species other than taro. This approach is termed heterologous hybridisation-probe analysis. With chloroplast and mitochondrial DNA probes, from spinach and maize respectively, differences were observed between *C. esculenta* and *C. gigantea*, but not between varieties of *C. esculenta*. Tests with mitochondrial rDNA suggested, surprisingly, that mitochondria in *C. gigantea* are less closely related to mitochondria in *C. esculenta* than they are to mitochondria in *Alocasia brisbanensis*, another member of the tribe Colocasioideae. More investigation is needed to develop tests for chloroplast and mitochondrial variation within *C. esculenta*.

Tests with a 5S ribosomal DNA probe, from the nuclear genome of rye, demonstrated that the 5S rDNA locus in taro is structurally similar to 5S loci in other plants. Although not examined further, 5S rDNA has potential as marker of intraspecific genotypic variation.

Using 18S rDNA from the *Nor*-locus of wheat as a probe, variation was detected in an initial survey of a small number of taro varieties (variants)¹⁾. Very frequent mutation during vegetative reproduction, and amplification of new variants to detectable levels, would make *Nor*-locus rDNA variation unsuitable for investigating the long-term dispersal of taro. A variable, but not too variable, genotypic marker is required. Sexual reproduction by triploid taro in New Zealand is unknown (Matthews 1985), and the three phenotypically distinct variants found in New Zealand were tested with rDNA fragments cloned from taro (homologous hybridisation-probe analysis). No intravarietal differences

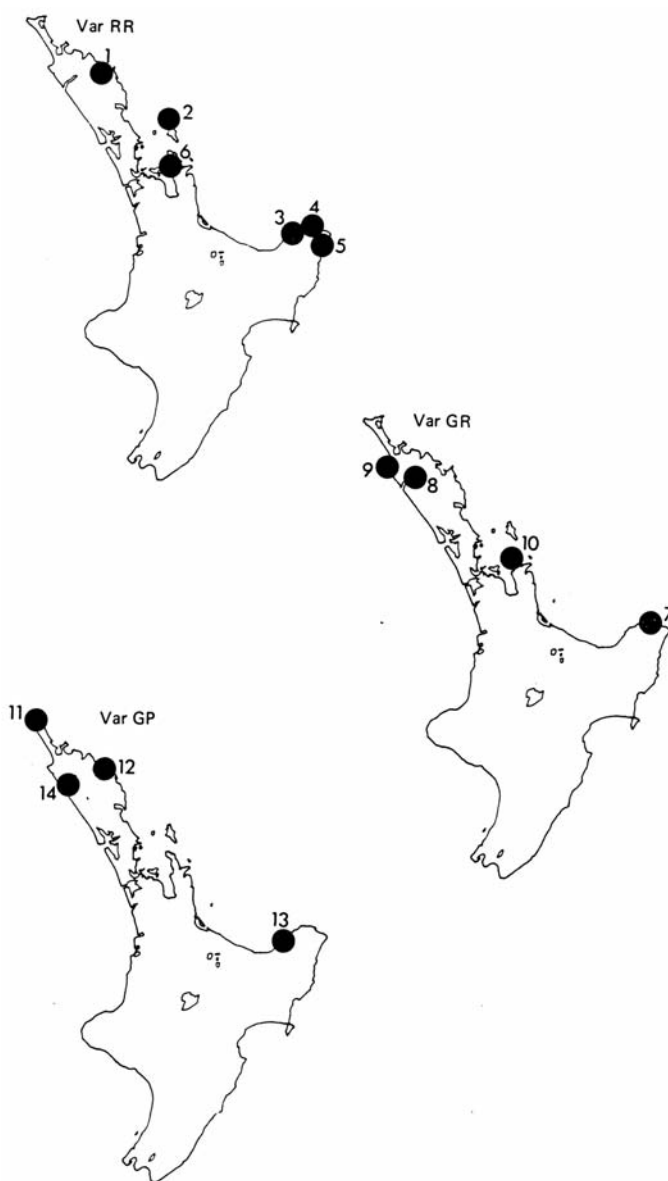


Figure 11.1 Sites of triploid taro variants RR, GR, GP from North Island, New Zealand, analysed with taro rDNA probes. For sites 1–14, the variant, Canberra accession number (T) with location, habitat, and chromosome number are as follows. Var. RR: 1 = T272, Okokako Road, Bay of Islands, wild, $2n = 42$; 2 = T274, Whangapoua Beach, Coromandel Peninsula, wild, $2n = 42$; 3 = T275, Putanga, East Cape, wild; 4 = T276, non-cultivated garden, Te Hekawa, East Cape, $2n = 42$; 5 = T277, Hamana Stream, East Cape, wild, $2n = 42$; 6 = T278, Port Charles, Coromandel Peninsula, garden, $2n = 42$. Var. GR: 7 = T279, Te Hekawa, East Cape, garden, $2n = 42$; 8 = T281, Reena, Hokianga, wild; 9 = T282, Waihopo, Aupouri Peninsula, garden, $2n = 42$; 10 = T283, Colville, Coromandel Peninsula, garden, $2n = 42$. Var. GP: 11 = T284, Kapowairua, North Cape, wild, $2n = 42$; 12 = T 286, Te Arakanihi, Bay of Islands, wild, $2n = 42$; 13 = T287, Rerepa Street, East Cape, wild, $2n = 42$; 14 = T288, Reena, Hokianga, wild.

were found among geographically wide-spread samples of each phenotypic variety in New Zealand. The stability of rDNA variants, thus indicated, encouraged further investigation of rDNA variation on a wider geographical scale (see later chapters).

11.2 Materials and Methods

Materials and methods were largely as described in Chapter Ten. To test for intra- and interspecific variation, small numbers of diverse samples were surveyed first. If variation were found, then the same test combination of restriction enzyme and probe was applied to plants from a wide geographical range. The initial tests included diploid ($2n = 28$) and triploid ($2n = 42$) taro varieties from different locations (various Canberra collection numbers), another species (*C. gigantea*, Canberra collection T268, from an ornamental collection in Australia), and another genus (*Alocasia brisbanensis*, Canberra collection T222, wild from the Windsor Tableland, northeast Queensland, Australia).

A. brisbanensis A. Hay is an Australian species previously known by the name *A. macrorrhizos* (L.) G. Don, but separated by Hay and Wise (1989) into a supra-generic 'Ozarum group', distinct from the 'Macrorrhizos group' containing *A. macrorrhizos* (L.) G. Don and *A. flabellifera* A. Hay. The latter, known only from Papua New Guinea, also includes plants previously identified as *A. macrorrhizos* (Hay and Wise 1989). Samples of three New Zealand variants of *C. esculenta* were distributed in the field as shown in Figure 11.1.

11.2.1 Probes and wash conditions

During the preliminary experiments, a range of low to moderate stringency wash conditions were tried for filters after Southern transfer and hybridisation. The conditions recorded below do not represent the only successful wash conditions tried for each probe after hybridisation with taro DNA, and do not represent optimised conditions. Autoradiographic exposure times varied from hours to several days.

(1) Chloroplast DNA probe, *Sal* I-6 (Figure 11.2): *Sal* I fragment 6 (9 kbp) from the single copy region of the chloroplast genome of *Spinacia oleracea* (spinach), ligated with pBR322. Donated by P. R. Whitfield (C.S.I.R.O., Canberra, Australia). Washed twice with a solution of 2x SSC, 0.1% SDS, pre-heated to 55°C, 15 minutes per wash.

(2) Mitochondrial DNA probe, *Cox* I (Figure 11.3: 10 kbp *Bam* HI fragment from the mitochondrial genome of *Zea mays*, *cms-c* variety (maize), ligated with pUC19. Donated by C. S. Levings (North Carolina State University, Raleigh, U.S.A.). Contains the 1.5 kbp gene for subunit I of cytochrome oxidase (*Cox* I) and flanking regions (Isaac et al. 1985). Washed four times with a solution of 2x SSC, 0.1% SDS, pre-heated to 65°C, 15 minutes per wash.

(3) Mitochondrial DNA probe, 18-5S rDNA (Figure 11.3): 6 kbp *Bam* HI fragment from the mitochondrial genome of *Zea mays* (maize, variety not specified), ligated with pUC9. Donated by C. S. Levings. Contains 18S and 5S rDNA genes and flanking sequence (Chao et al. 1984). Washed two times with a solution of 2x SSC, 0.1% SDS, pre-heated to 65°C, 15 minutes per wash, and two times with a solution of 0.2x SSC,

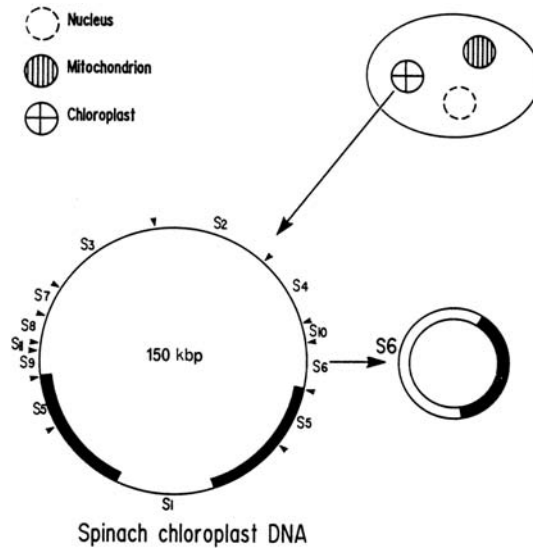


Figure 11.2 Derivation of a chloroplast DNA probe (*Sal* I-6) by ligation of *Sal* I fragment 6 (S6), from spinach chloroplast DNA, into a plasmid (lower right). Chloroplast restriction site map adapted from Herrmann et al. (1980).

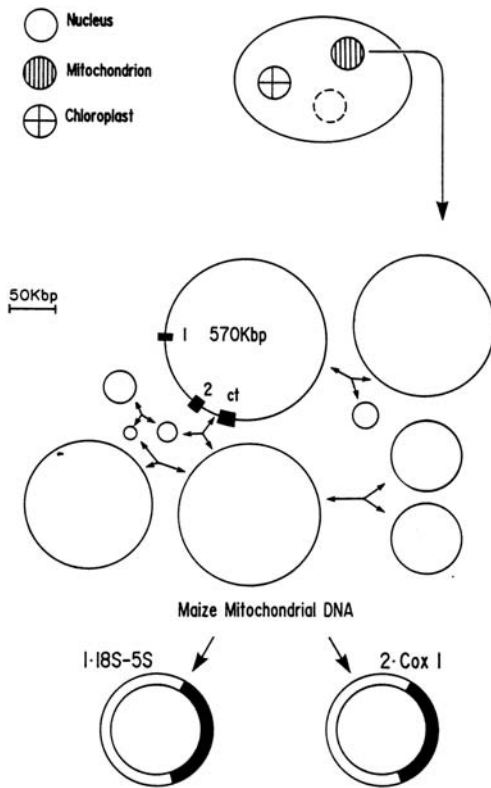


Figure 11.3 Derivation of mitochondrial DNA probe fragments ligated into plasmids (below) from *Zea mays* mtDNA (above). Cell components at top (schematic). *Cox* I = cytochrome oxidase subunit I gene; 18S-5S-chloroplast rRNA genes. Adapted from Lonsdale et al. (1984) and Dawson et al. (1986). The large circle of 570 kbp contains the entire sequence complexity of the genome. Intra-molecular recombination is believed to cause the breakdown of the large circle into a heterogeneous population of subgenomic circles. Mitochondria have a major role in ATP production and oxygen consumption (metabolic energy transfer), and every cell contains a population of mitochondria, the number varying between cell types. In most plants, each mitochondrion contains a heterogeneous population of mtDNA molecules.

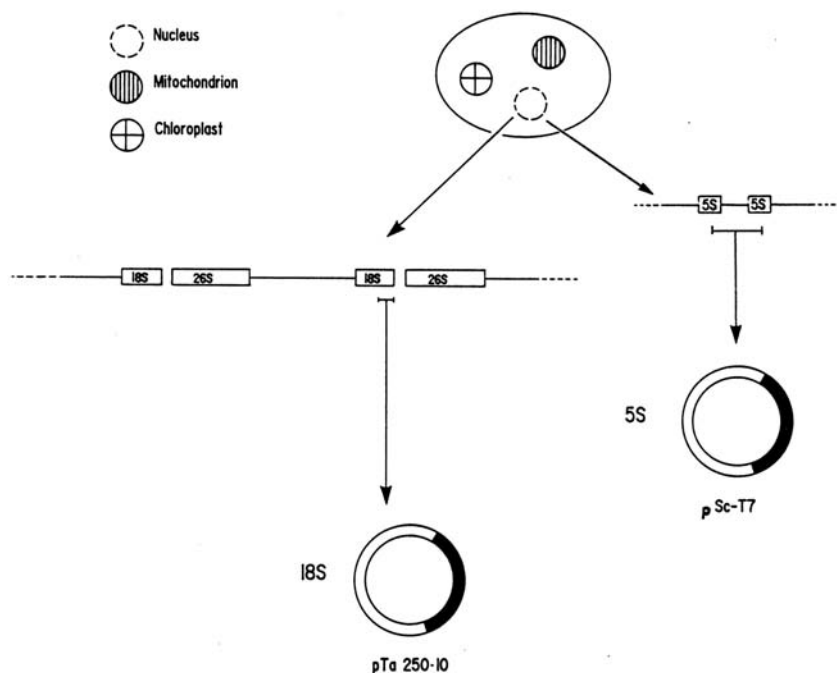


Figure 11.4 Derivation of nuclear rDNA probes. The plasmid pTA250.10 contains a fragment of 18S rDNA from the nuclear genome of *Triticum aestivum*. The plasmid pSc-T7 contains an entire 5S rDNA repeat from the nuclear genome of *Secale cereale*. Cell components at top (schematic) Ribosomal DNA diagrams not to scale. The 18S and 5S rRNA genes are located at different chromosomal loci within nuclear genomes.

0.1% SDS, pre-heated to 65°C, 15 minutes per wash.

(4) Nuclear 5S rDNA probe, Sc-T7 (Figure 11.4): 0.5 kbp *Bam* HI fragment containing an entire 5S rDNA repeat unit, from a nuclear chromosome of *Secale cereale* (rye), ligated with pBR322 (Lawrence and Appels 1986). Donated by R. Appels (C.S.I.R.O., Canberra, Australia). Washed four times with a solution of 2x SSC, 0.1% SDS, pre-heated to 65°C, 15 minutes per wash.

(5) Nuclear 18S rDNA probe, pTA250.10 (Figure 11.4): 1 kbp *Taq* I fragment from the 18S rDNA gene, from a nuclear chromosome *Nor*-locus of *Triticum aestivum* cv Chinese Spring (wheat), ligated with pBR322. Donated by R. Appels. Washed four times with a solution of 3x SSC, 0.1% SDS, pre-heated to 65°C, 15 minutes per wash.

(6) Nuclear rDNA probe pCe34.1: 5.5 kbp *Eco* RI fragment, from a nuclear chromosome of *C. esculenta* (taro), and containing the entire intergenic spacer region and flanked by parts of the 26S and 18S rDNA genes; ligated with pBR322 (cloning, see Chapter Ten; description, see Chapter Twelve). Washed four times with a solution of 2x SSC, 0.1% SDS, pre-heated to 65°C, 15 minutes per wash.

11.3 Results

The number of different DNA fragment classes, and their overall size ranges, are given in summary tables. This information is useful for choosing appropriate electrophoretic conditions and DNA size standards (individual estimates of DNA fragment sizes were not sufficiently accurate to justify detailed reporting).

(1) *Spinach chloroplast DNA probe, Sal I-6* (Table 11.1). With each of the five tests (*Bam* HI, *Eco* RI, *Hind* III, *Sal* I and *Xho* I) no differences were found between five varieties of *C. esculenta*. With *Bam* HI and *Eco* RI, *C. esculenta* gave restriction fragment patterns different from those of *C. gigantea*.

(2) *Maize mitochondrial DNA probe, Cox I* (Table 11.2, Figure 11.5). No differences were found between four varieties of *C. esculenta* or between *C. esculenta* and *A. brisbanensis* after *Eco* RI digestion. Only partial *Eco* RI digestion was achieved for *C. gigantea* (Figure 11.5), but the result nevertheless suggests that there is no difference between this and the other two species. Tests with *Msp* I and *Hae* II revealed differences between *C. esculenta*, *C. gigantea*, and *A. brisbanensis*, but no differences among seventeen accessions of *C. esculenta*. Tests with *Bam* HI also revealed no differences among the seventeen accessions of *C. esculenta*.

(3) *Maize mitochondrial DNA probe, 18-5S rDNA* (Table 11.3, Figure 11.6). Tests with *Bam* HI and *Hae* III revealed no differences between *C. gigantea* and *A. brisbanensis*, but did reveal differences between these species and *C. esculenta*. No differences were found among the eleven accessions of *C. esculenta* tested with *Bam* HI, and no differences were found among the fourteen accessions tested with *Hae* III.

(4) *Rye nuclear 5S rDNA probe, Sc-T7* (Figure 11.7). Two triploid varieties of *C. esculenta* produced regular ladders of *Bam* HI fragments based on multiples of 200 bp, indicating that the 200 bp sequence is a high copy-number unit tandemly repeated at one or more loci. Complete digestion of all repeats by *Rsa* I generated a single 200 bp band.

(5) *Wheat nuclear 18S rDNA probe, pTA250.10* (Figure 11.8). In an initial test with *Eco* RI, two varieties of *C. esculenta* produced a constant smaller band (4.0 kbp) and a variable larger band (5.5 and 6.0 kbp). No obvious size differences were found between two accessions of the phenotypic variety GP (T287, T284) from different locations. *C. gigantea* also produced a 4.0 kbp band, together with a large, 7.1 kbp band. Thirteen further accessions of *C. esculenta* from Papua New Guinea, Australia, the Philippines, and New Zealand were tested with *Eco* R.I. Variation of fragments larger than 4.0 kbp was found to be common, within the size range 5.5–6.0 kbp, and all the accessions displayed the 4.0 kbp size class. Because the experimental conditions for this preliminary survey gave poor resolution of size differences, details of the results are not presented.

(6) *Taro nuclear rDNA probe, pCe34.1*. Analysis of three triploid varieties of *C. esculenta* from New Zealand:

All accessions of var. RR and var. GR (six and three, respectively) gave the same pattern of *Taq* I fragments, different from the one pattern produced by the four accessions of var. GP (Figure 11.9). The *Taq* I fragments are generated from the intergenic spacer region of *Nor*-locus rDNA (see Chapter Twelve).

All accessions of var. RR and var. GR (six and four, respectively) gave the same pattern of *Rsa* I fragments after partial digestion, different from the one pattern produced by the four accessions of var. GP (Figure 11.10). The ladders of partial digestion products reflect the distribution of *Rsa* I sites throughout the rDNA repeat sequence. At least some of the variability of *Rsa* I fragments arose in the intergenic spacer region (see Chapter Twelve). In theory, variability also could have arisen in other parts of the rDNA repeat sequence. The survey of *Rsa* I partial-digestion products indicates that the overall rDNA repeat sequence is conserved between different accessions within each phenotypic variety (RR, GR, GP), and between varieties (RR, GR).

All accessions of var. RR and var. GR (six and four, respectively) gave the same pattern of *Bam* HI fragments, different from the one pattern produced by the four accessions of var. GP (Figure 11.11). The large and variable *Bam* HI fragments span the entire intergenic spacer region (see Chapter Twelve). *Bam* HI fragment length differences, between varieties (GP versus RR and GR) and between doublets within individual samples (RR and GR), appear directly correlated with the intergenic spacer variation exhibited by *Taq* I fragment length differences in the same set of samples (compare Figure 11.9 and 11.10).

Table 11.1 DNA restriction fragments from *C. esculenta* and *C. gigantea*, detected by hybridisation with spinach chloroplast DNA probe (*Sal* I-6). No variation was observed among varieties of *C. esculenta*. The two species gave different *Bam* HI and *Eco* RI patterns.

A. Number of different fragments, and their approximate size range in kbp, after digestion with five restriction enzymes (? = unclear results, – = no test).

B. Accessions tested (tests performed, T collection number, species and variety, somatic cell chromosome number, source, and collection date). Source abbreviations: Q = Queensland. NI = North Island. * = unprovenanced collections from botanical gardens or private collections.

A

Test enzyme	<i>C. esculenta</i>		<i>C. gigantea</i>	
	No. fragments	Size range kbp	No. fragments	Size range kbp
1. Bam HI	6	1.5–5.8	4	1.5–4.0
2. Eco RI	5	0.9–5.0	?	?–5.2
3. Hind III	2	8.5–10.8		
4. Sal I	3	6.4–16.0		
5. Xho I	3	6.2–13.0		

B

Tests	T. collection number	Name	2n=	Source	Collection date
1, 2	268	<i>C. gigantea</i>	–	Australia, Q.*	1985
2	110	<i>C. esculenta</i>	42	Indonesia, Timor	c.1963
1–5	277	<i>C.e.</i> var. RR	42	New Zealand, NI	1983
1–5	281	<i>C.e.</i> var. GR	42	New Zealand, NI	1983
1–5	284	<i>C.e.</i> var. GP	42	New Zealand, NI	1982
2	287	<i>C.e.</i> var. GP	42	New Zealand, NI	1983
1–5	289	<i>C.e.</i> var. AKL34	28	New Zealand, NI	1982

Table 11.2 DNA restriction fragments from *C. esculenta*, *C. gigantea*, and *A. brisbanensis*, detected by hybridisation with the *Cox I* mitochondrial DNA probe from maize. No variation was observed among varieties of *C. esculenta*. The *Eco RI* pattern for *C. gigantea* was not resolved (= ?) because of partial digestion, but was probably the same as for the other two species (see Figure 11.5). Different patterns were observed for each species with the enzymes *Msp I* and *Hae III*.

A. Number of different fragments, and their approximate size range in kbp, after digestion with four restriction enzymes.

B. Accessions tested (tests performed, T collection number, species and variety, somatic cell chromosome number, source, and collection date). Source abbreviations: Q = Queensland, PNG = Papua New Guinea, EHP = Eastern Highlands Province, NT = Northern Territory, WHP = Western Highlands Province, ESP = Eastern Sepik Province, NI = North Island. * = unprovenanced collections from botanical gardens or private collections.

A

Test enzyme	<i>C. esculenta</i>		<i>C. gigantea</i>	
	Fragments	kbp	Fragments	kbp
1. <i>Eco RI</i>	4	0.3–5.1	?	?
2. <i>Msp I</i>	6	0.4–2.1	5	0.4–3.4
3. <i>Hae III</i>	5	0.3–5.6	6	0.3–5.6
4. <i>Bam HI</i>	5	2.1–8.6	–	–

B

Tests	T. coll. number	Name	2n=	Source	Coll.date
1–3	222	<i>A. brisbanensis</i>	–	Australia, Q.	1985
2, 3	268	<i>C. gigantea</i>	–	Australia, Q.*	1986
2–4	11	<i>C. esculenta</i>	28	PNG, EHP	1982
2–4	21	<i>C. esculenta</i>	–	PNG, Moresby	1982
2–4	23	<i>C. esculenta</i>	28	PNG, Moresby	1982
2–4	31	<i>C. esculenta</i>	28	Australia, NT	1980
2–4	40	<i>C. esculenta</i>	–	Australia, Q.*	1981
2–4	42	<i>C. esculenta</i>	28	Australia, Q*	1981
2–4	49	<i>C. esculenta</i>	28	PNG, WHP	1982
2–4	50	<i>C. esculenta</i>	–	PNG, WHP	1982
2–4	152	<i>C. esculenta</i>	–	Philippines, Luzon	1985
2–4	225	<i>C. esculenta</i>	–	PNG, Moresby	1985
2–4	238	<i>C. esculenta</i>	–	PNG, ESP	1981
2–4	240	<i>C. esculenta</i>	–	PNG, ESP	1981
2–4	277	<i>C. e.</i> var. RR	42	New Zealand, NI	1983
2–4	281	<i>C. e.</i> var. GP	42	New Zealand, NI	1983
1–4	284	<i>C. e.</i> var. GP	42	New Zealand, NI	1983
1–4	287	<i>C. e.</i> var. GP	42	New Zealand, NI	1983
1–4	289	<i>C. e.</i> var. AKL34	28	New Zealand, NI	1982

Table 11.3 DNA restriction fragments from *C. esculenta*, *C. gigantea*, and *A. brisbanensis*, detected by hybridisation with the maize mitochondrial 18–5S rDNA probe. No variation was observed among varieties of *C. esculenta*. The *Bam* HI and *Hae* III patterns for *C. esculenta* differed from the patterns for *C. gigantea* and *A. brisbanensis*, and no differences were found between the latter two (see Figure 11.6).

A. Number of different fragments, and their approximate size range in kbp, after digestion with two restriction enzymes.

B. Accessions tested (tests performed, T collection number, species and variety, somatic cell chromosome number, source, and collection date). Source abbreviations: Q = Queensland, PNG = Papua New Guinea, EHP = Eastern Highlands Province, NT = Northern Territory, WHP = Western Highlands Province, ESP = Eastern Sepik Province, NI = North Island. * = unprovenanced collections from botanical gardens or private collections.

A

Test enzyme	<i>C. esculenta</i>		<i>C. gigantea</i>		<i>A. brisbanensis</i>	
	Fragments	kbp	Fragments	kbp	Fragments	kbp
1. Bam HI	3	3.3–8.6	3	3.3–11.6	3	3.3–11.6
2. Hae III	2	0.7, 2.1	2	0.7, 2.6	2	0.7, 2.6

B

Tests	T. collection number	Name	2n =	Source	Collection date
1, 2	222	<i>A. brisbanensis</i>	–	Australia, Q	1985
1, 2	268	<i>C. gigantea</i>	–	Australia, Q*	1986
2	11	<i>C. esculenta</i>	28	PNG, EHP	1982
1, 2	21	<i>C. esculenta</i>	–	PNG, Moresby	1982
1, 2	23	<i>C. esculenta</i>	28	PNG, Moresby	1982
1, 2	31	<i>C. esculenta</i>	28	Australia, NT	1980
1, 2	40	<i>C. esculenta</i>	–	Australia, Q*	1981
2	42	<i>C. esculenta</i>	28	Australia, Q*	1981
1, 2	49	<i>C. esculenta</i>	28	PNG, WHP	1982
2	50	<i>C. esculenta</i>	–	PNG, WHP	1982
2	225	<i>C. esculenta</i>	–	PNG, Morobe	1985
1, 2	238	<i>C. esculenta</i>	–	PNG, ESP	1981
1, 2	240	<i>C. esculenta</i>	–	PNG, ESP	1981
1, 2	277	<i>C. e. var. RR</i>	42	New Zealand, NI	1983
1	281	<i>C. e. var. GR</i>	42	New Zealand, NI	1983
1, 2	284	<i>C. e. var. GP</i>	42	New Zealand, NI	1982
1, 2	289	<i>C. e. var. AKL34</i>	28	New Zealand, NI	1982

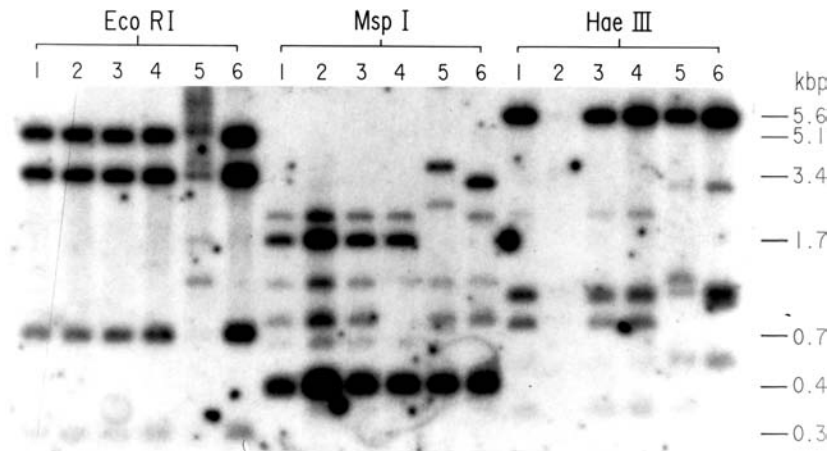


Figure 11.5 DNA fragments from *C. esculenta*, *C. gigantea*, and *A. brisbanensis* detected by hybridisation with the *Cox* I mitochondrial DNA probe from maize. Extracts of total DNA were digested with *Eco* RI, *Hsp* I, and *Hae* III. Lanes 1–4, *C. esculenta* (1–T289, 2–294, 3 = 277, 4–T281). Lane 5, *C. gigantea* (T268). Lane 6, *A. brisbanensis* (T222).

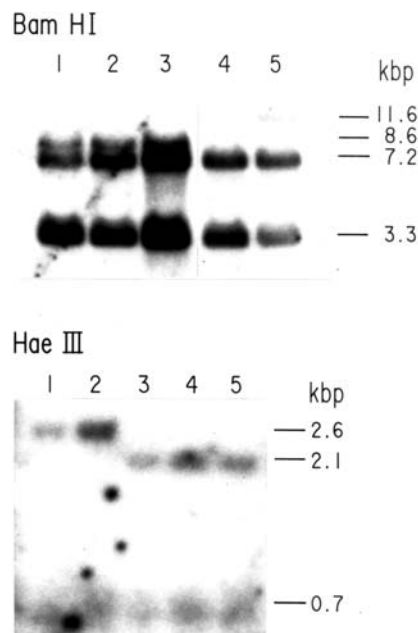


Figure 11.6 DNA fragments from *C. esculenta*, *C. gigantea* and *A. brisbanensis* detected by hybridisation with the mitochondrial 18–5S rDNA probe from maize. Total DNA extracts were digested with *Bam* HI and *Hae* III. Samples for *Bam* HI: lanes 13, *C. esculenta* (1 = T277, 2 = T43, 3 = T23); lane 4, *C. gigantea* (T268); lane 5, *A. brisbanensis* (T222). Samples for *Hae* III: lane 1, *C. gigantea* (T268); lane 2, *A. brisbanensis* (T222); lanes 3–5, *C. esculenta* (3 = T238, 4 = T31, 5 = T11)

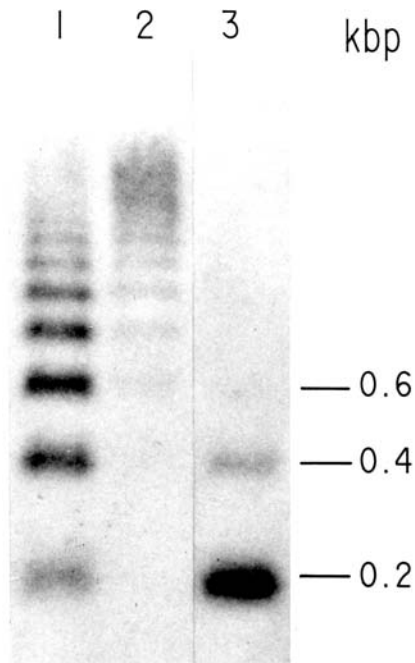


Figure 11.7 DNA fragments from two varieties of *C. esculenta*, detected by hybridisation with the 5S rDNA probe (Sc-T7) from *Secale cereale*. Lane 1: T281 (var. GR, $2n = 42$, New Zealand) digested with *Bam* HI. Lane 2: T264 (var. *fontanesii*, $2n = 42$, Australia) digested with *Bam* HI. Lane 3: T281 digested with *Rsa* I. The fragments in lane 1 (bp, approximate only) form a ladder of monomers (200 bp), dimers (400 bp), trimers (600 bp), and so on.

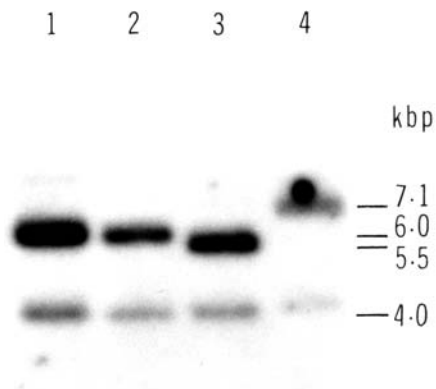


Figure 11.8 Taro DNA fragments detected with the nuclear rDNA, 18S gene probe from wheat (pTA250.10), after digestion of total DNA with *Eco* RI. Samples: (1) T287, *C. esculenta* var. GP, $2n = 42$, New Zealand, (2) T284, *C. esculenta* var. GP, $2n = 42$, New Zealand, (3) T289, *C. esculenta* var. AKL 34, $2n = 28$, New Zealand, (4) T268, *C. gigantea*, Australia.

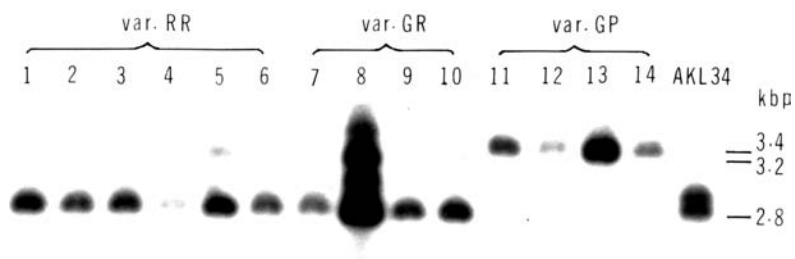


Figure 11.9 Ribosomal DNA spacer fragments from New Zealand triploid varieties RR, GR, and GP (sites 1–14), and the diploid AKL34. Autoradiograph of *Taq* I fragments after Southern transfer and probing with pCe34.1. One sample of var. GR, from site 8, gave partial digestion products because of excess DNA, together with the bands expected for this variety. See Figure 11.1 for site locations.

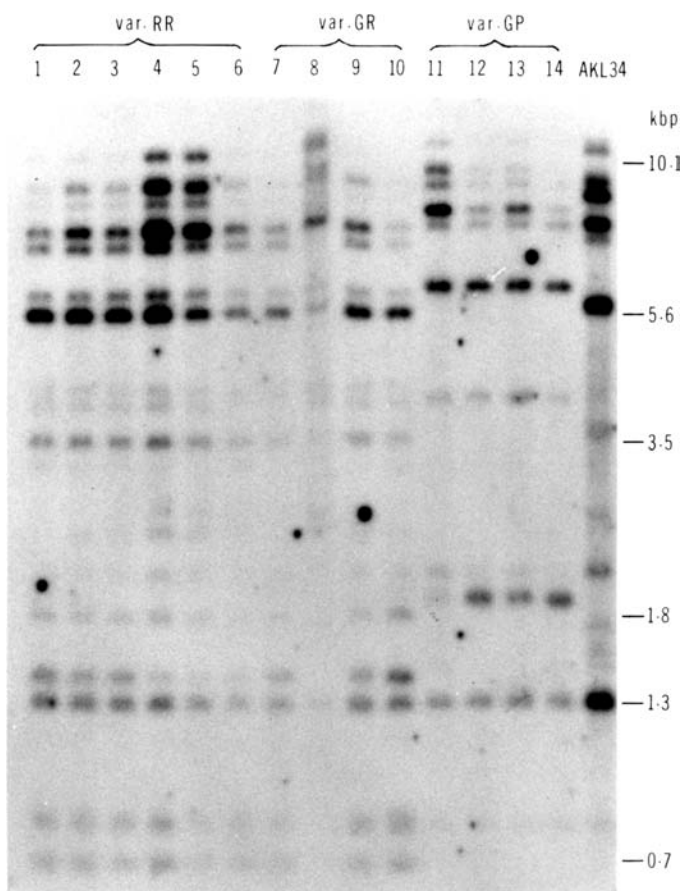


Figure 11.10 Ribosomal DNA spacer and genic fragments from New Zealand triploid varieties RR, GR, and GP (sites 1–14), and the diploid AKL34. Autoradiograph of *Rsa* I fragments (partial digestion products) after Southern transfer and probing with pCe34.1. See Figure 11.1 for site locations.

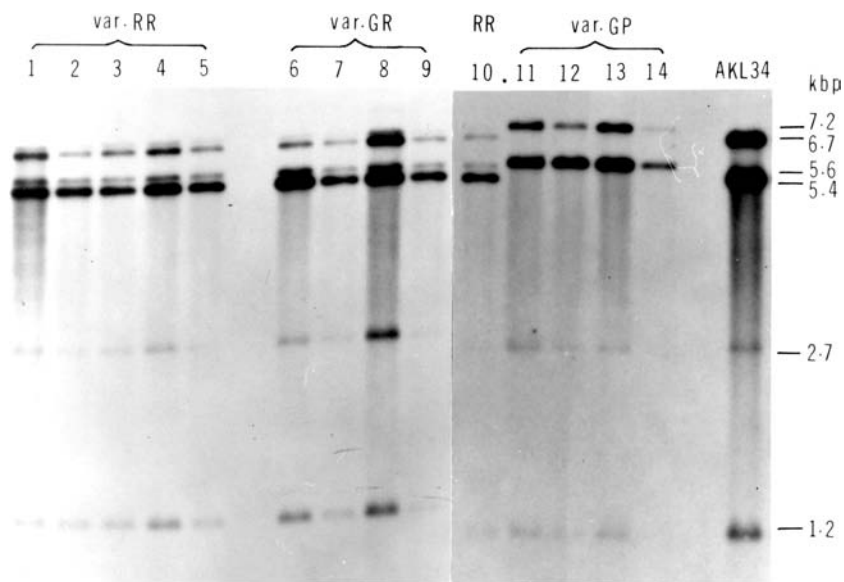


Figure 11.11 Ribosomal DNA variation in New Zealand triploid varieties RR, GR, and GP (sites 1–14), and the diploid AKL34. Autoradiograph of *Bam* HI fragments after Southern transfer and probing with pCe34.1. See Figure 11.1 for site locations. The large and variable fragments in the upper part of the autoradiograph span the intergenic spacer regions of rDNA repeats.

11.4 Concluding Discussion

After considering the identity of DNA fragments detected by hybridisation-probe analysis, comparisons are made between varieties of *C. esculenta*, and between *C. esculenta*, *C. gigantea*, and *A. brisbanensis*. The stability of rDNA in clonal lineages of taro is discussed in relation to the survey of vegetative clones from New Zealand.

11.4.1 The identity of fragments detected by hybridisation-probe analysis of total DNA

Within a broad classification of life forms, taro belongs to the plant eukaryotes, organisms with cells in which there are three kinds of organelle containing a DNA genome. The organelles are the nucleus, the mitochondrion, and the chloroplast. Total-DNA prepared from taro thus contains DNA from each of these organelles. In theory, DNA fragments from one or more organelle might be detected simultaneously by hybridisation-probe analysis of total-DNA extracts. In general it is most likely that probes derived from chloroplast, mitochondrial, and nuclear DNA hybridise most strongly to fragments from the chloroplast, mitochondrial, and nuclear genomes respectively, but cross-hybridisation between genomes is theoretically possible because of (1) common ancestry (endosymbiotic evolution) and (2) DNA exchange between genomes.

The endosymbiotic theory

Nuclear, mitochondrial, and chloroplast genomes are generally believed to have a common ancestry (Figure 11.12). Although the details of this ancestry are by no means clear, the serial endosymbiosis theory illustrated in Figure 11.12 is strongly supported by comparisons of the structure, biochemistry, and genotypic variation of cells and organelles in a broad range of life forms (Taylor 1979; Dayhoff and Schwartz 1980; Doolittle and Bonen 1981; Küntzel and Köchel 1981; Pace et al. 1986; Cavalier-Smith 1987). As a consequence of this evolutionary history, sequences similar to the probe sequence might have been inherited from a very ancient genome by more than one kind of organelle in taro. However, considering the time involved, hundreds of millions of years, only extremely stable sequences would be sufficiently similar for detectable cross-hybridisation between a probe from one genome and a target sequence from another.

Analyses of various highly conserved (stable) rRNA genes have been important for recent development of the endosymbiotic theory because rRNA genes occur in the genomes of each lineage involved — in the eukaryotic nuclei, in mitochondria and chloroplasts, and in the prokaryotes (Pace et al. 1986; Sogin and Gunderson 1987). For higher plants, the various studies have shown that, first, mitochondria and chloroplasts are both more closely related to bacterial prokaryotes than they are to plant nuclei; and second, that the mitochondria and chloroplasts represent separate, monophyletic lineages (Palmer 1985). In practice, under the kinds of experimental conditions described in this chapter, cross-hybridisation due to ancient shared ancestry is either absent, or too weak, to confuse identification of total-DNA fragments detected by hybridisation probe analysis, even when nuclear or mitochondrial rDNA probes are used.

The exchange of DNA sequences between genomes

Exchanges of various DNA sequences between nuclear, mitochondrial, and chloroplast genomes have been reported for a range of plant species (Stern and Palmer 1984; Whisson and Scott 1985), and are illustrated schematically in Figure 11.12. The phylogenetic history and molecular mechanisms for reported exchanges are unclear at present, but many different kinds of exchange are evident, and exchange in general is probably a continuing and common phenomenon in plants (Stern and Palmer 1984).

An example of particular interest is reported by Stern and Lonsdale (1982) who found, in *Zea mays*, a 12 kbp fragment of chloroplast-like DNA in purified mitochondrial DNA (Figure 11.3). This fragment has a base sequence more than 90% similar to the corresponding sequence in maize chloroplasts. Within the 12 kbp fragment, a sequence was found that hybridised strongly to chloroplast 16S rDNA, and weakly to functionally homologous, structurally similar, mitochondrial 18S rDNA. Detailed analysis confirmed the presence in maize mitochondria of a 16S rDNA sequence, which must have come from a chloroplast.

It is evident from the above that any probe DNA sequence has some chance of hybridising to fragments from any kind of genome in a total-DNA extract, regardless of how variable or stable that sequence might have been in the past. The genomic locations of fragments are not proven by hybridisation probe analysis of total-DNA extracts alone.

Genomic locations can be investigated by (1) analysis of total-DNA in conjunction with controlled breeding trials, using progeny analysis to determine the mode of genetic transfer, usually maternal for chloroplasts and mitochondria, and biparental for nuclear chromosomes, with Mendelian frequencies for alleles on nuclear chromosomes, (2) analysis of DNA purified from each organelle, and (3) *in situ* hybridisation. In Chapter

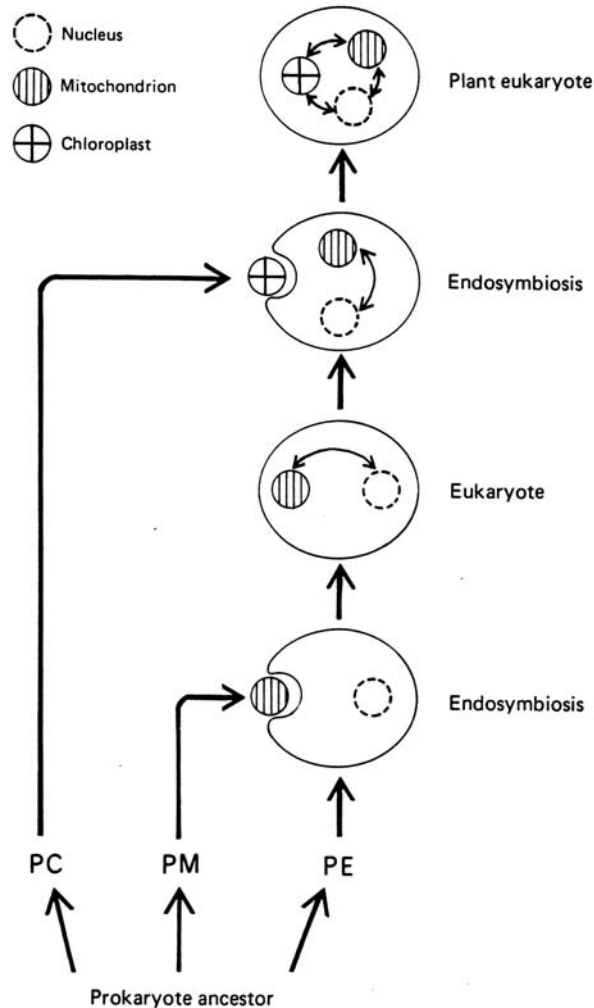


Figure 11.12 Evolutionary scheme (serial endosymbiosis hypothesis) for plant eukaryotes, adapted from Taylor (1976) and Doolittle and Bonen (1981). PM = protomitochondrial symbiont. PC = protochloroplast endosymbiont. PE = protoeukaryote. The early evolution of prokaryotes and of the nuclear genome are unresolved in this scheme. Arrows within cells indicate possible movements of DNA sequences between co-existing genomes. Symbioses may have occurred independently more than once for both kinds of endosymbiosis shown.

Twelve, *in situ* hybridisation of the taro rDNA probes to nuclear chromosomes is demonstrated.

11.4.2 Intraspecific comparisons

In recent years, much has been learned about the general qualities of variation in chloroplast and mitochondrial DNAs (for reviews, see Birky 1978; Palmer 1985, 1987; Sederoff 1987; Zurawski and Clegg 1987; Palmer and Herbon 1988). Both chloroplast DNA (cpDNA) and mitochondrial DNA (mtDNA) undergo slow rates of base substitution. Plant mitochondrial genomes are generally composed of variously-sized circles (for example, see Figure 11.3) among which recombination occurs. These complex genomes evolve rapidly in structure, but slowly in sequence (Palmer and Herbon 1988). Palmer (1987) notes that chloroplast genomes are always composed of one large circular molecule (for example, see Figure 11.2), which evolves very slowly with infrequent rearrangements (inversions and transpositions). Insertions or deletions of extremely short sequences (one to ten base pairs) are the most common form of CPDNA mutation. The overall slow rate of change makes the CPDNA genome most valuable for studies aimed at the species level or above, although intraspecific variation has been reported for a few species (Palmer 1987; Neale et al. 1988). Phylogenetic analysis of plant mtDNA variation is severely limited by the high frequency of confounding rearrangements (Palmer 1987; Palmer and Herbon 1988). Nevertheless, the relatively frequent rearrangement of plant mtDNA improves the chance of detecting different maternal lineages within a species, and mapping their geographical distributions, with or without phylogenetic interpretation. For example, patterns of mtDNA variation in *Zea mays* subspecies *trates* (maize and teosinte) closely parallel those of whole plant and cytological variation (Timothy et al. 1979; Weissinger et al. 1983).

In the preliminary experiments with chloroplast and mitochondrial DNA probes, no variation was observed among different accessions, phenotypic varieties, and chromosome number variants of taro. Few tests were performed, so it is still quite possible that chloroplast and mitochondrial DNAs do vary in different lineages of taro. Two general strategies can be envisaged for future tests with heterologous probes. The first strategy is to continue tests with probes which have already revealed interspecific variation (see below). Further restriction enzymes could be used with these probes to localise the variable sequences, and to examine them closely in different varieties of taro. Locations of interspecific variation may also be locations at which intraspecific variation is functionally permissible and likely to occur. The second strategy is to continue testing previously untried combinations of probe and enzyme. According to the general views of chloroplast and mitochondrial DNA variation, noted above, restriction fragment differences between varieties of a species are most likely to reflect length differences (insertions, deletions), or inversions, rather than single base-pair changes. Any enzyme that cuts left and right of a length difference, or of an inversion break point, is potentially able to reveal the difference. Initially, therefore, it may be more profitable to try many new probes with just a few enzymes, rather than using a wide range of enzymes with each new probe.

The rye nuclear 5S rDNA probe and *Bam* HI were used to test two phenotypically distinct triploid varieties (Figure 11.7). Incomplete (partial) digestion with *Bam* HI generated ladders of similar periodicity for both varieties (Figure 11.7). Partial digestion by the methylation-sensitive *Bam* HI is attributed to 5-methylcytosine residues at the GGATCC *Bam* HI recognition sequences, as demonstrated for 5S rDNAs from other plant species (Goldsborough et al. 1982; Rafalski et al. 1982; Reddy and Appels 1989). Only the large multimers were produced by var. *fontanesii* (Figure 11.7), possibly as an artefact of reaction conditions. *Rsa* I digestion of taro 5S rDNA was complete and confirmed the monomer size of 200 bp. In other plants, single *Bam* HI and *Rsa* I sites occur in the highly conservative genic region of 5S repeat units, and the taro 5S rDNA unit can be aligned by analogy as shown in Figure 11.13.

Both intra- and interspecific variation have been detected in many grass species of the tribe Triticeae, but different species within one genus (*Secale*) could not be unambiguously differentiated even with extensive sequence analysis (Reddy and Appels 1989). Analysis of 5S rDNA could be useful for studying the evolution of taro, but it is not clear *a priori* what kind of information would be obtained.²⁾

The spacer sequences of 5S rDNAs accumulate mutations in the form of base

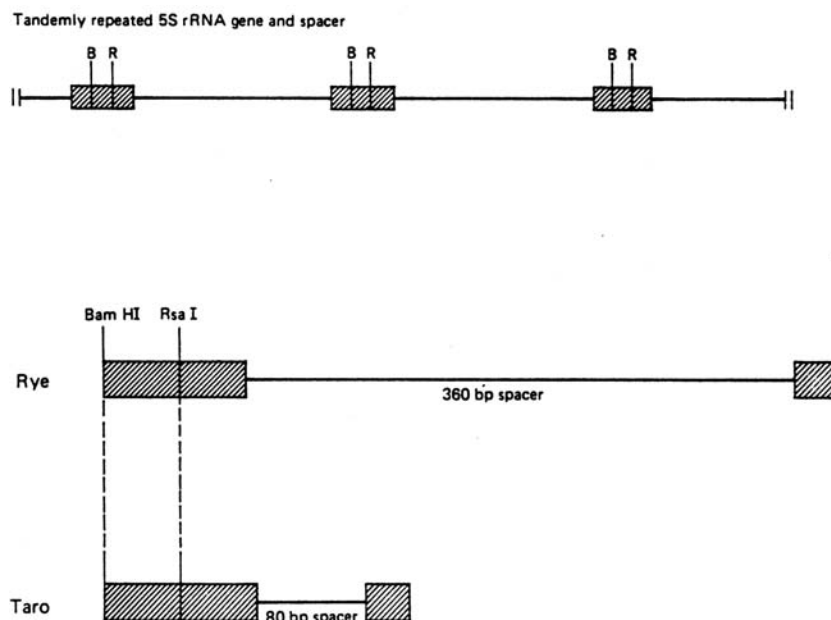


Figure 11.13 Alignment of *C. esculenta* (taro) and *Secale cereales* (rye) 5S rDNA repeat units, as suggested by the presence of single *Bam* HI and *Rsa* I restriction sites in taro 5S rDNA. The 5S rRNA gene of taro is assumed to be 120 bp long, as in rye and in plants and animals generally. Map for the rye repeat unit adapted from the full nucleotide sequence published by Reddy and Appels (1989).

substitutions, duplications, deletions, and insertions, with only minor heterogeneity in the gene region (see Reddy and Appels 1989, with references). The 5S rRNA gene of plants and animals is generally 120 bp in size (Scoles et al. 1988), and if the size estimate for the entire taro 5S repeat is correct, then a spacer sequence of only 80 bp can be inferred (Figure 11.13). This is very short compared to the 340 to 360 bp spacer sequences reported by Reddy and Appels (1989) for *Secale* sp. If 5S spacers are generally very short in *C. esculenta*, but are subject to insertions and deletions of similar size to those reported for the Triticeae, then finding phylogenetically informative base substitutions might be difficult. On the other hand, insertions and deletions could provide useful typological markers for different 5S rDNA lineages, with or without phylogenetic interpretation. Tests with the wheat 18S rDNA probe and *Eco* RI (Figure 11.8) provided the first indication of intraspecific variation, and for this reason, and because of their size (two fragments spanning a complete repeat sequence), *Eco* RI fragments were chosen as targets for cloning. Wheat rDNA probes were also used to screen *Eco* RI fragments from taro during the cloning process (see Chapter Ten). The cloned *Eco* RI rDNA fragments from taro were then used to test for variation among New Zealand triploid varieties (section 4, below).

11.4.3 Inter-specific comparisons

With the mitochondrial probe *Cox* I and the enzymes *Msp* I and *Hae* III, differences were found between each of the three species examined (Figure 11.5). With the mitochondrial 18–5S rDNA probe, similar *Bam* HI and *Hae* III fragments were detected for *C. gigantea* and *A. brisbanensis*, different from the fragments produced by *C. esculenta* (Figure 11.6). In each of these comparisons, some DNA fragments did not vary between species, and when *Eco* RI fragments were probed with *Cox* I, no variation was detected (Figure 11.5). The dendrogram constructed from these results (Figure 11.14) suggests that mitochondria in *C. gigantea* are less closely related to mitochondria in *C. esculenta* than they are to mitochondria in *A. brisbanensis*. The apparent close relationship of *C. gigantea* and *A. brisbanensis* could be due to convergent mutational events within the history of either species. Alternatively, if the classification correctly reflects the overall phylogeny of mitochondria in these taxa, then there may have been introgression of mitochondria from one species lineage to another, or variant mitochondrial lineages may have existed within ancestral populations prior to the differentiation of *Colocasia* and *Alocasia*.

It is perhaps significant that Engler and Krause (1920) placed *C. gigantea* Hook. f. (synonymous with *C. indica* [Lour.] Hassk) in Section ‘Caulescentes’, separate from three other commonly collected species, *C. esculenta*, *C. affinis*, and *C. fallax*. These three were placed together in the Section ‘Tuberosae’. *C. gigantea* differs strikingly from the other *Colocasia* species in morphological aspects of the leaf, inflorescence, fruit, and seed (Engler and Krause 1920; and personal observation). Although *C. gigantea* is not obviously like *Alocasia* species phenotypically, its designation as a member of *Colocasia* should perhaps be questioned, considering the affinity between its mitochondria and those of *Alocasia*.

The kinds of mutation that created differences between *Colocasia* species and *A.*

brisbanensis cannot be described yet. Intraspecific rearrangements of a sequence immediately adjacent to the *Cox I* gene, in varieties of *Zea mays*, were reported by Isaac et al. (1985), and possible mechanisms and controlling factors for the rearrangements were suggested. These included specific mitochondrial sequences thought to promote recombination and undefined controls by nuclear genomes on the constitution of mitochondrial genomes. Given the rapid rate of plant mitochondrial DNA change (see Section 2 above), it cannot be assumed that the same recombination processes and nuclear influences operate in taxa that are distantly related, such as *Colocasia* and *Alocasia*. Using a maize *Cox I* mitochondrial DNA probe to survey total-DNA extracts, Breiman (1987) found intra- and interspecific variation among species of *Aegilops*, and no variation among species of *Triticum* (wheat) that shared the AB haploid genome

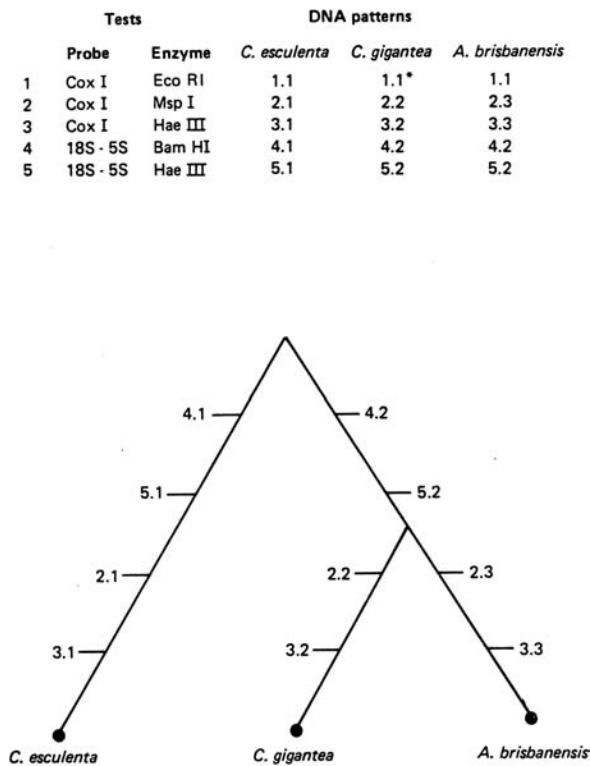


Figure 11.14 Dendrogram for species of *Colocasia* and *Alocasia*, based on restriction fragment patterns detected with mitochondrial DNA probes from maize. Results from Figures 11.5 and 11.6.

A. Five tests, each characterised by the probe and the restriction enzyme used. The different patterns that resulted are each identified by a test and pattern number. The tests represents characters, and the patterns are the observed character states. Asterisk: result same as for the other species, but interpretation based on partial digestion products.

B. Dendrogram based on the distribution of variable character states among species.

(nuclear chromosomal complement). Whatever the causes for variation in different taxa, it appears that the *Cox I* gene and its flanking regions will be useful generally for investigating intra- and interspecific evolution.

Palmer (1985) reviewed observations of chloroplast genomes in diverse taxa. In the relatively conservative genomes of chloroplasts, length mutation is the most common kind of mutation. Very short length mutations of a few base pairs occur predominantly in non-coding regions, and larger length mutations of 50–1200 bp are often found to cluster in relative ‘hotspots’, usually at the two ends of the large single copy region. The spinach chloroplast DNA probe *Sal I*-6 used here (Figure 11.2) is derived from one end of the large single copy region, and the different DNA patterns detected for *C. esculenta* and *C. gigantea* (Table 11.1) probably reflect length mutations in the same region of *Colocasia* chloroplast genomes.

11.4.4 Ribosomal DNA stability in clonal lineages

The generation of a new detectable and heritable rDNA variant requires that there be (1) mutation, (2) intracellular amplification within the genome, and (3) a positive bias in the reproduction of cells containing the variant (sorting out), in generative vegetative meristems and/or the germlines leading to gametes (eggs and pollen). These processes are poorly understood (see Chapter Nine), and when beginning the study of taro, little could be assumed about the stability of rDNA in clonal lineages.

The question of stability within clonal lineages is of concern for two reasons. First, mutation might occur after collection in the field, during the study, because of inherent genetic instability or in response to the study protocol (live field collections were maintained for up to four years by vegetative propagation, prior to testing). Second, the study is primarily concerned with the long term history of taro within the human era, and the vegetative propagation of cultivars is a major component of this history. If ribosomal DNA changed frequently during vegetative reproduction, then it would be of little use for tracing the long-term dispersal history of cultivated taro.

It is commonly thought that genomes do not change during clonal reproduction. This view is most commonly expressed as an implicit assumption (e.g., see Ellstrand and Roose 1987) or expressed summarily in textbook definitions of clonal reproduction (e.g., Weier et al. 1974; Briggs and Walters 1984; Mayo 1987). The observation that genomes in general are stable during clonal reproduction does not necessarily apply to specific components of a specific genome. Ribosomal DNA mutation during vegetative reproduction (mitosis in non-floral, generative apices) does not appear to have been the subject of direct experimental investigation, although this would be possible with the test system established by Durrant (1962) with *Linum usitatissimum* (cultivated flax). Environmentally induced and heritable effects on ribosomal DNA copy number were found by Cullis (1979) using varieties produced by Durrant (1962), but the observed effects cannot be ascribed to a particular stage in the flax life cycle because the original treatments (Durrant 1962: 29) spanned both pre-floral and floral stages. The opportunity to assess the stability of rDNA variants during vegetative reproduction was presented by New Zealand collections of *C. esculenta* varieties RR, GR, and GP, described by

Matthews (1984, 1985).

Ribosomal DNA was surveyed in three phenotypically distinct triploid varieties (RR, GR, GP) in accessions from a wide geographical range within New Zealand (Figure 11.1). No variation was observed in tests which examined the intergenic spacer region specifically (*Taq* I fragments, Figure 11.9), unmapped *Rsa* I recognition sites scattered through the spacer and genic regions of rDNA repeats (Figure 11.10), and the overall length of rDNA repeats (*Bam* HI fragments, Figure 11.11). The lack of rDNA variation within varieties is interpreted as evidence for rDNA stability during vegetative reproduction. This interpretation follows from observations of taro reproduction in New Zealand, and two assumptions discussed below.

Seed production by taro in New Zealand has never been reported, although flowering is common (Cooper 1969; Matthews 1984) and reproduction appears to be obligately vegetative. Likely reasons are the short summer growth period, which may not be long enough for seed development, and the fact that the varieties under consideration are triploid (Matthews 1985). In winter in New Zealand, the growth of taro slows down and frequently ceases completely (personal observation), and it is a general observation for plants that triploids are either completely or predominantly sterile (a single extra set of chromosomes results in irregular chromosome pairing during meiosis). The three phenotypically distinct varieties are therefore thought to represent three different clonal lineages.

The degree of clonal stability indicated by the observations of rDNA homogeneity depends on the interpretation of when the triploid varieties were introduced. If prehistoric, the introductions could have been as early as c. 800 to 1000 years ago, according to archaeological estimates of human occupation dates (Trotter 1982; Caughley 1988). Alternatively, it has been suggested that these varieties could have been imported from China by merchants supplying immigrant market gardeners, sometime between the turn of the century and the 1930s (Yen and Wheeler 1968). The wide distributions of the varieties (Matthews 1985), and local information supplied to this author at a number of field sites, make it certain that triploid taro arrived before World War II (1939). There is no evidence for variation arising within the course of the study, and ribosomal DNA patterns in New Zealand appear to have been stable for a period of at least fifty years.

Interpreting the results as a test of clonal stability requires two assumptions: (1) there were not multiple introductions of genotypically similar clones, derived from different sexual progeny produced outside New Zealand, and (2) homogeneity within the varieties distinguished here did not arise through the convergence of separate clonal lineages. If there were multiple introductions of a particular variety, then it seems more probable that they came from one clonal lineage, established in cultivations in the area of origin, than from separate but genotypically similar clonal lineages. The second assumption is made because it is hard to imagine how convergence could occur on all clonal branches of different lineages without the survival of intermediate and progenitor rDNA patterns in many branches.

To conclude, the survey of New Zealand triploid varieties indicated that rDNA is sufficiently stable for use as a genotypic marker for the dispersal of clonal lineages, and

attention was turned next to a wider survey of Asian and Pacific taro, described in the following chapters.

Notes

- 1) In this volume, the term ‘variant’ is used as an equivalent to ‘variety’ as an informal term, not as a formal botanical term.
- 2) Using 5S rDNA genic-region primers and the Polymerase Chain Reaction (PCR), Nakayama et al. (2008) amplified 5S repeats in a wild taro from Myanmar and found a simple ladder pattern like the one reported here. The basic repeat unit was found to be 210 bp, and the PCR products formed a 210, 420, 630 bp... ladder. The PCR products were sequenced, showed variation within a single population (represented by seeds from one location), and were used for *in situ* hybridisation to chromosomes, revealing the cytological locus of 5S repeats.

Chapter Twelve

The *Nor*-Locus Ribosomal DNA Repeat Unit of *C. esculenta*

12.1 Introduction

As described in the previous chapter, *Eco* RI digestion and hybridisation probe analysis with a wheat rDNA probe revealed large taro fragments (c.a. 5.6–6.0 kbp) that varied in size between taro varieties, and smaller fragments (c.a. 4.0 kbp) that were invariant. One large and one small *Eco* RI fragment were cloned from AKL 34, a New Zealand diploid taro variety. The recombinant bacterial plasmids containing the taro rDNA fragments were named pCe34.1 and pCe34.2 respectively (see Chapter Ten). Restriction enzyme digests and double-digests of the cloned rDNA fragments, and of total-DNA extracts from AKL 34, were probed with previously defined wheat rDNA probes to locate the restriction enzyme sites and approximate gene positions in taro rDNA. These experiments confirmed the expectation that the large *Eco* RI fragments from taro contain the intergenic spacer region, and consistent with this were later observations that pCe34.1, and a 2.8 kbp *Taq* I fragment excised from pCe 34.1, could be used as probes to detect small and highly variable *Taq* I, *Hinf* I, and *Rsa* I fragments (see last part of Chapter Eleven; and Chapter Fourteen). Variation in the large intergenic spacer region was expected because it is generally observed within and between eukaryote species (see Chapter Nine). Restriction site mapping was also performed using pCe34.1 and pCe34.2, and the 2.8 kbp *Taq* I fragment excised from pCe34.1, to probe digests of the cloned rDNA fragments and digests of total DNA from AKL 34.

A cloned rDNA fragment from taro variety AKL 34 was hybridised *in situ* to chromosomes from mitotically dividing root-tip cells of AKL 34. Two major chromosomal loci were found associated with the microscopically visible clear areas within the cell nuclei, which indicate functionally active nucleoli where rDNA is transcribed to produce rRNA. The results described in this chapter provide a structural and functional basis for relating observations of rDNA variation in taro to the many reports of *Nor*-locus rDNA in other organisms. Taro rDNA does not appear at all unusual, and this simplifies the interpretation of rDNA variation in taro and its near relatives in the chapters that follow.

12.2 Materials and Methods

The diploid ($2n = 28$) taro variety AKL 34 was collected from a house garden in Northland, New Zealand, in 1982 and was described by Matthews (1984). Two *Eco* RI fragments spanning the taro rDNA repeat unit were independently cloned from AKL 34 using the vector pBR322 and *Escherichia coli* strain RR1. The cloning protocol, described

in Chapter Ten, was similar to that used by Appels et al. (1987), with minor modifications. Extraction of total-DNA and of plasmids containing the rDNA sequences, restriction enzyme digestion, electrophoresis, Southern transfer, and autoradiography were performed as described in Chapter Ten.

To map restriction enzyme sites and gene positions, the following enzymes and enzyme combinations were used, and the digestion products electrophoresed side-by-side: *Eco* RI, *Bam* HI, *Eco* RI + *Pst* I, *Bam* HI + *Pst* I, *Eco* RI + *Xba* I, *Bam* HI + *Xba* I, *Eco* RI + *Kpn* I, *Bam* HI + *Kpn* I, *Bam* HI + *Eco* RI. In separate experiments, with the taro 2.8 kbp *Taq* I fragment from pCe34.1 as probe, the enzymes *Taq* I, *Hinf* I, *Taq* I + *Hinf* I, and *Rsa* I were used. Wheat rDNA clones from the PTA recombinant plasmid series, described by Appels and Dvorák (1982 a, b), were kindly supplied by R. Appels: pTA250.1 (4.4 kbp *Bam* EI/*Eco* RI fragment spanning the large intergenic spacer), pTA250.2 (3.6 kbp *Bam* HI fragment spanning most of the rRNA gene region), pTA250.3 (0.9 kbp *Bam* UI/*Eco* RI fragment from the 26S gene), pTA250.10 (1.0 kbp *Taq* I fragment from the 18S rRNA gene), and pTA250.11 (0.5 kbp *Taq* I fragment from the 26S rRNA gene). For restriction site mapping, digests of the cloned rDNA fragments and of total DNA from AKL 34 were probed with pCe34.1, pCe34.2, and the 2.8 kbp *Taq* I fragment excised from pCe34.1, resulting in the plasmid pCe34.11 (Chapter Ten) and providing probe rDNA for later surveys of intergenic spacer variation in taro (Chapter Fourteen).

For *in situ* hybridisation of a cloned rDNA sequence to chromosomes, the methods of Appels et al. (1978) and McIntyre (1987) were followed. Synthesis of ³H-labelled copy-RNA probes from pCe34.1, preparation of chromosomes from mitotically dividing root-tip cells, hybridisation, and autoradiography were as described in Chapter Ten.

12.3 Results

12.3.1 Mapping

A 2.8 kbp *Taq* I fragment from pCe34.1 was mapped to the large intergenic spacer region as shown in Figure 12.1. When used as a probe, the 2.8 kbp *Taq* I fragment hybridised strongly to two doublets composed of *Bam* HI/*Pst* I fragments, generated by double digestion of total-DNA with *Bam* HI and *Pst* I. Weak hybridisation to the *Pst*/*Eco* fragment was seen with digests of the cloned insert, and no hybridisation to this fragment was detected with total-DNA digests. This may be because of either (1) a very small amount of overlap by the 2.8 kbp *Taq* I fragment, or (2) the presence of divergent sub-repeat sequences on both sides of the *Pst* I site.

The experiments with wheat and taro rDNA probes, and with cloned rDNA and native total-DNA, gave mutually consistent results, and these are summarised as a single map for an entire repeat unit (Figure 12.2). Because pCe34.1 and pCe34.2 were independently prepared from total-DNA extracts, they contain rDNA sequences that were almost certainly not from the same repeat unit *in vivo*. Mapping of the two cloned fragments and of rDNA in total-DNA extracts confirmed that pCe34.1 and pCe34.2 are typical for rDNA repeats in AKL 34. The rDNA fragments from these clones can

therefore be shown as adjacent to each other, for schematic purposes (Figure 12.2). By analogy to maps for restriction sites and rRNA genes in other genera (*Triticum* and *Pisum*), the boundaries of the large intergenic spacer and the rRNA genes of taro can be shown as in Figure 12.3.

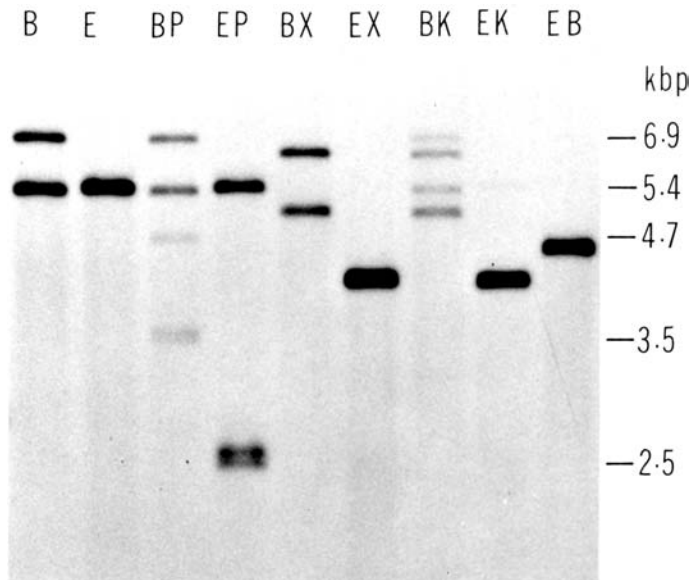


Figure 12.1 Mapping the position of the 2.8 kbp *Taq* I fragment from pCe34.1. This fragment was used to probe total DNA extracts from AKL 34, after digestion with the same set of enzymes used for restriction-site mapping. The position of the *Taq* I fragment is revealed by reference to the map shown in Figure 12.2. The enzymes used and the fragments detected are listed below. The 5' to 3' orientations of double-digestion fragments are indicated in brackets: the first letter indicates the 5' restriction enzyme site, and the second letter indicates the 3' restriction enzyme site (see Figure 12.2). Asterisks refer to the 26S gene *Bam* HI site which is not cut in all repeat units.

B = *Bam* HI; 6.9 kbp, 5.4 kbp.

E = *Eco* RI; 5.5 kbp.

BP = *Bam* HI + *Pst* I; doublet, approx. 4.7 kbp (BP); doublet, approx. 3.5 kbp (*BP); plus undigested *Bam* HI fragments.

EP = *Eco* RI + *Pst* I; doublet, approx. 2.5 kbp (EP); plus undigested *Eco* RI fragments.

BX = *Bam* HI + *Xba* I; 6.5 kbp (BX); 5.0 kbp (*BX).

EX = *Eco* RI + *Xba* I; 4.2 kbp (EX).

BK = *Bam* HI + *Kpn* I; 6.4 kbp (BK); 4.9 kbp (*BK); plus undigested *Bam* HI fragments, the results of partial digestion by *Kpn* I.

EK = *Eco* RI + *Kpn* I; 4.1 kbp (EK); plus faint band of undigested *Eco* RI fragments, the result of partial digestion of *Kpn* I.

BE = *Bam* HI + *Eco* RI; 4.4 kbp (EB).

The doublet *Bam* HI/*Pst* I fragments span the region from two 26S gene *Bam* HI sites, one of which is not cleaved in all repeat units, to the spacer region *Pst* I site (Figure 12.2). AKL 34 possesses two rDNA size variants which differ by approximately 100 bp, and the difference resides within the intergenic spacer region spanned by the *Bam* HI/*Pst* I fragments. Similar size variation was seen after *Hinf* I and *Rsa* I digestion of total DNA from AKL 34, using the 2.8 kbp *Taq* I spacer fragment as probe. This probe also detected an approximately 1.5 kbp fragment in an *Rsa* I digest of the cloned sequence in pCe34.1, and fragments of 1.5 kbp and 1.6 kbp after *Rsa* I digestion of total DNA from AKL 34. The cloned sequence thus appears to be derived from the smaller rDNA variant found in AKL 34. The relative positions of *Taq* I and *Hinf* I intergenic spacer sites (Figure 12.4) were determined by single and double digestion of total DNA. The 5' to 3' orientation of these sites within repeat units, and their exact positions relative to *Rsa* I sites, have not been determined. The 100 bp spacer difference lies within the 2 kbp sequence shared by the *Taq* I and *Hinf* I fragments. The 1.5 1.6 kbp *Rsa* I fragments must be derived from entirely within the variable 2 kbp region, as suggested in Figure 12.4, or from partly within it.

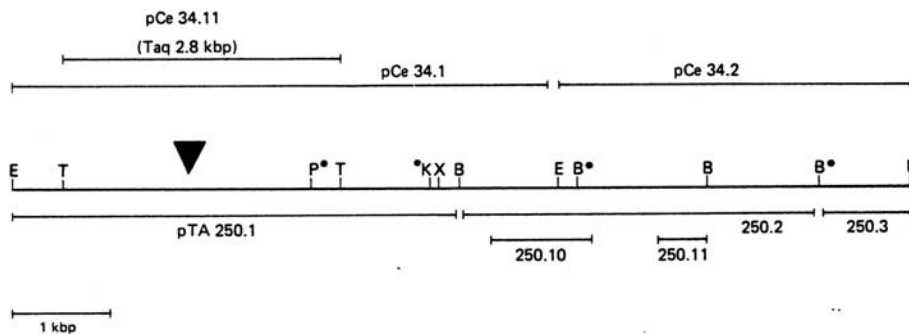


Figure 12.2 Restriction-site map for *Nor*-locus rDNA from taro variety AKL 34, orientation 5' to 3' (left to right), wheat determined with rDNA probes. Restriction endonucleases: E = *Eco* RI, T = *Taq* I, P = *Pst* I, K = *Kpn* I, X = *Xba* I, B = *Bam* HI. Asterisks mark sites which consistently failed to be cut in a high proportion of repeat units in total-DNA extracts. pCe = taro rDNA clone: the 2.8 kbp *Taq* I fragment was used as a probe after excision from pCe34.1. Wheat rDNA probes: pTA250.10 marks the 3' end of the 18S rRNA gene, pTA250.11 marks the 5' end of the 26S rRNA gene, and pTA250.3 is close to the 3' end of the 26S rRNA gene.

Two rDNA variants detected in total-DNA extracts from AKL 34 are distinguished by an approximately 100 bp size difference located between the *Taq* I sites (arrow). The exact position is not known. *Taq* I sites 5' and 3' to the 2.8 kbp fragment give many very small fragments which have not been mapped. The 2.8 kbp *Taq* I fragment hybridised strongly to the *Eco*/*Pst* (5'-3') fragment in digests of cloned insert and total DNA, and is therefore shown located over this fragment.

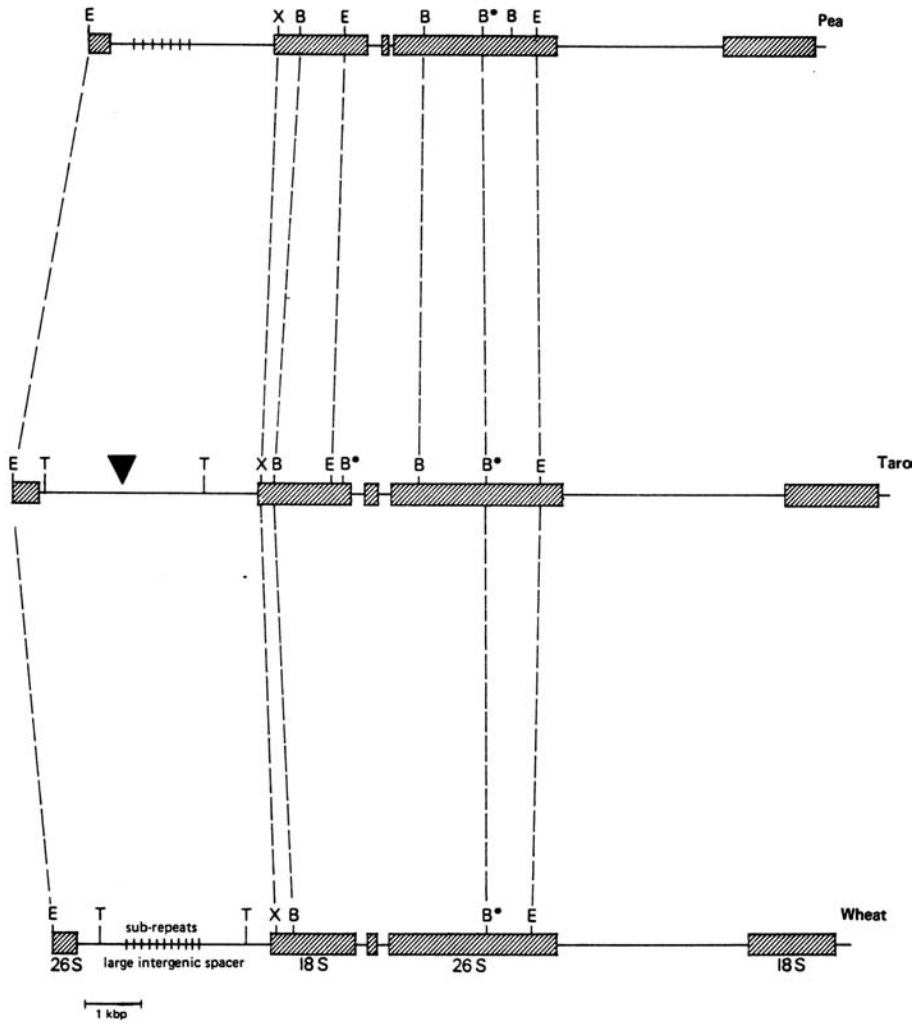


Figure 12.3 Alignment of the taro rDNA restriction site map with maps for *Pisum sativum* (pea) and *Triticum aestivum* (wheat).

The boundaries for the rRNA genes in taro are not known exactly, but are presumed to be similar to the boundaries indicated for pea and wheat, since the overall arrangement of rRNA genes, and the large intergenic spacer, is the same in these three species and eukaryotes generally. The dotted lines connect what are believed to be conserved (homologous) restriction sites. Asterisks mark sites which are consistently not cut in a high proportion of repeat units, in extracts of total DNA. This phenomenon has been reported in pea, wheat, and other plant species, and is a further indication of homology (see text). An arrow marks the variable region of taro rDNA, which correspond, in position, to the variable spacer sub-repeat regions of pea and wheat. The pea map is compiled from Jorgensen et al. (1987) and Kaufman et al. (1987), and the wheat map is compiled from Appels et al. (1980), Appels and Dvořák (1982a), and Jorgenson et al. (1987).

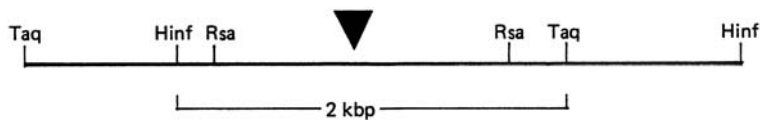


Figure 12.4 Restriction site map for a variable segment in the large intergenic spacer region, for taro variety AKL 34, 5' to 3' orientation not determined. The exact positions of *Rsa* I sites relative to *Taq* I and *Hinf* I sites are not known. The *Rsa* I fragment may lie within or overlap the central *Taq* I/*Hinf* I fragment. The arrow marks the approximate location of a 100 bp size difference observed between rDNA variants in total-DNA extracts from AKL 34. Within rDNA repeats, there are many other *Taq* I, *Hinf* I, and *Rsa* I sites outside the spacer segment shown here.

12.3.2 *In situ* hybridisation to chromosomes in the cells of root-tips

At interphase, during the cell life cycle, chromosomes are uncoiled and cannot be visualised as individual entities. However, nucleoli are visible at interphase and mark the sites of ribosomal RNA synthesis from rDNA (Novikoff and Holtzman 1976). After *in situ* hybridisation with copy rRNA from pCe34.1, autoradiographic grains were visible in the nucleoli of interphase cells (Figure 12.5). These grains were arranged in two distinct clusters, suggesting the existence of two separate chromosomal loci for rDNA.

Mitotic cell division is the basis for vegetative reproduction, and for the differentiation of roots and other plant parts. There are four phases during mitotic cell division: prophase, metaphase, anaphase, and telophase. During prophase, chromosomes are visible in partially condensed form, each having doubled during late interphase (the S period), giving one parent and one daughter chromatid. During metaphase the chromosomes condense further, become aligned on the mitotic spindle, and display clearly distinct chromatids. In subsequent phases, the chromatids separate and the division of the nucleus and cytoplasm produces two daughter cells. *In situ* hybridisation of the copy rRNA probe to prophase and metaphase chromosomes (Figure 12.5) revealed two major chromosomal loci for rDNA on separate chromosomes. These loci correspond to the two areas of dispersed grains seen in the nucleoli of interphase cells.¹⁾

12.4 Concluding Discussion

Spacer length variation in taro is probably due to the presence, and variation in number, of sub-repeat units, as reported for pea (sub-repeat unit of 180 bp) and wheat (sub repeat unit of 130 bp). The size difference of approximately 100 bp in spacer fragments from AKL 34 is probably due to differences of one or very few sub-repeat units.

The *Taq* I sites that border highly variable regions in the spacer regions of taro and wheat (Figure 12.3) are the result of convergent (parallel) evolution. Spacer regions and their sub-repeat structure are conserved as structural components of *Nor*-locus rDNAs, but the base sequences within them vary greatly among diverse taxa (Appels and Honeycutt 1986). Ribosomal DNA sequence divergence between taxa is greatest in the sub-repeat arrays, relative to genic regions and other parts of the large intergenic spacer

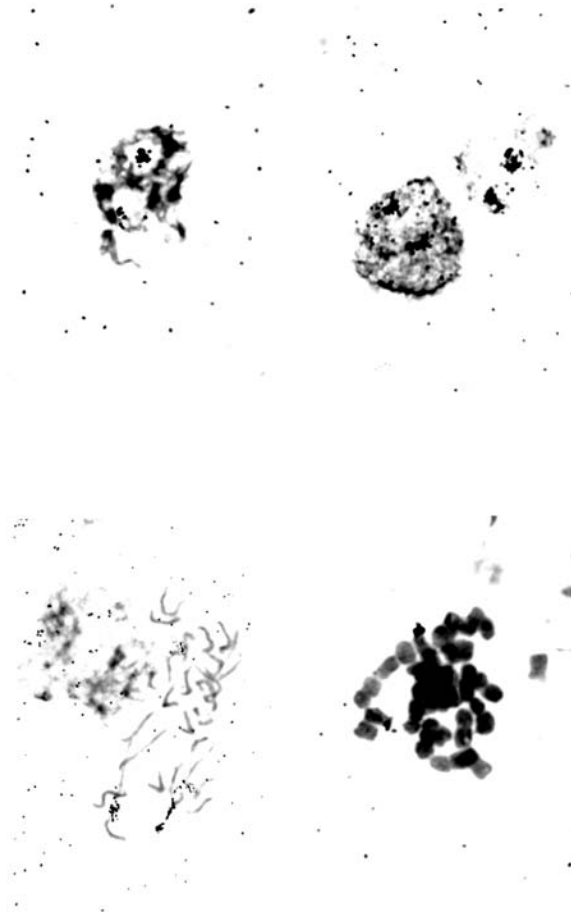


Figure 12.5 Taro rDNA probe from variety AKL 34 (5.5 kbp *Eco* RI fragment) hybridised *in situ* to mitotic chromosomes from the same variety. Silver emulsion autoradiographs of chromosomes. Clusters of silver grains (black dots) mark the locations of two rDNA loci in each cell. The upper frames show interphase cells. Two clear areas mark nucleoli, in the cell at left, and each nucleolus contains one rDNA locus. The lower left frame shows contents of prophase cell, with silver grains dispersed along two partly condensed chromosomes; the lower right frame shows one metaphase cell, with one rDNA locus visible on each of two fully condensed chromosomes (at bottom left and top centre).

(see Chapter Nine, Figure 9.5, from Appels and Honeycutt 1986). It is likely that most rDNA differences detected among different varieties of taro (Chapters 11 and 14) are due to varying numbers of sub-repeats.

The *Taq* spacer fragment is produced in tests with wheat because the sub-repeat sequence lacks *Taq* I sites (Appels and Dvořák 1982a). Sub-repeats are probably present in taro rDNA, and the same explanation is suggested for *Taq* I, *Hinf* I, and *Rsa* I spacer fragments from taro (Figure 12.4). These three enzymes require specific sequences of

only four nucleotides to cleave DNA, and the four-base recognition sequences are very common. Cleavage of rDNA with these enzymes generates many very small fragments from regions outside the variable spacer region. In the future, mapping the positions of such common sites in rRNA genes may be particularly useful for close characterisation of different rDNA variants, because many sites are recognised and this increases the chance of detecting variation in conserved genic regions. One *Bam* HI site in the 26S rRNA gene remained uncleaved in a large proportion of rDNA repeats, and two *Bam* HI autoradiographic bands of approximately equal intensity resulted (Figure 12.1). A similar result has been reported for the same *Bam* HI site in many plant species, and various explanations have been proposed. These involve either base sequence change within the *Bam* HI recognition sequence, or a base modification by methylation that makes the enzyme recognition sequence resistant to cleavage. The latter explanation is favoured by most writers, although it does not exclude the possibility of base sequence changes having occurred. The argument for methylation is considered next.

Resistance to cleavage by *Bam* HI can be explained (Siegel and Kolacz 1983) by postulating the presence of a guanosine residue adjacent to the 3' cytosine in the *Bam* HI recognition sequence, GGATCC. The resulting CGG sequence would be a substrate for methylation. Jorgensen et al. (1987) noted that this explanation is consistent with the fact that the *Bam* HI site is detected in only about one half of the rDNA repeats in pea, as well as in wheat, barley, rye, corn, beans, and pumpkin. Taro and many other species can be added to this list. Gruenbaum et al. (1981) proposed that CCG sequences, when synthesised during DNA replication as copies of complementary GGC, will be methylated at one or other C at random, but not at both, resulting in 50% methylation at each cytosine. Since *Bam* HI is sensitive to methylation of the internal but not the external cytosine in its recognition sequence (McClelland 1983), Jorgensen et al. (1987) expected about half of the *Bam* HI sites adjacent to a G at the 3' end to be resistant to cleavage.

The postulated presence of guanosine adjacent to the 26S gene *Bam* HI site was confirmed in the rice 26S rDNA sequence published by Takaiwa et al (1985). Beginning at base number 1905, the sequence CGGATCCG was reported (*Bam* HI recognition sequence underlined). Because this is a palindrome, 50% of replications from either strand may generate an internal methylated cytosine in the *Bam* HI recognition sequence. The same eight base sequence is probably associated with the 26S gene *Bam* HI site (six bases) in taro.

A similar explanation to that just given may also apply to the *Bam* HI site in the taro 18S gene, and to the *Kpn* I recognition sequence (GGTACC), which is similar to that for *Bam* HI, and which is not detected in all taro rDNA repeats (Figure 12.1, *Kpn* I + *Bam* HI digest). The recognition sequence for *Pst* I (CTGCAG) contains methylation-sensitive cytosines and is located in the large intergenic spacer where the frequency of methylation may be related to regulation of rDNA transcription (von Kalm et al. 1986). In *Lilium henryi*, von Kalm et al. (1986) found a *Pst* I site in a consistently undermethylated region of the spacer, and a spacer *Kpn* I site, close to the 18S gene, was also detected in only a proportion of rDNA repeats from total-DNA extracts (Figure 12.6).

In situ hybridisation of the cloned 5.5 kbp *Eco* RI rDNA fragment demonstrated that

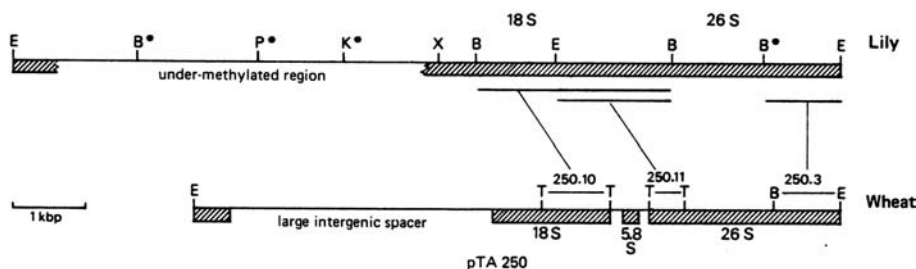


Figure 12.6 The rDNA repeat unit of *Lilium henryii* aligned with wheat rDNA probes from the pTA250 series (adapted from von Kalm et al. 1986). Asterisks mark sites for restriction enzymes that did not cleave the rDNA of all repeat units (see text for explanation). Restriction enzymes: E = *Eco* RI, B = *Bam* HI, K = *Kpn* I, X = *Xba* I, T = *Taq* I.

rDNA in the diploid taro variety AKL 34 is located in two major loci associated with nucleoli. The cloned rDNA is thus positively identified as the rDNA of nucleolar organiser regions (*Nor*-locus rDNA). Ribosomal DNA fragments detected in total DNA extracts with the cloned rDNA probes are mostly derived from the *Nor*-loci, since these are the major (large copy number) sites for rDNA. The two rDNA loci in AKL 34 are most simply interpreted as belonging to one homologous pair of chromosomes. However, it is possible for one of two homologous chromosomes to have no rDNA (a null locus), and a more complicated interpretation is that the rDNA loci in AKL 34 are on two heterologous chromosomes, with each locus paired by a null locus. The absence of *Nor*-locus rDNA within a chromosome complement (haploid set) has been reported for the toad *Xenopus* as a condition that is lethal in homozygous chromosomal combinations and viable in heterozygous combinations (Novikoff and Holtzman 1986: 335). Because cultivated taro is propagated vegetatively, non-lethal heterozygous conditions could have become common in cultivation, even if such conditions were rare in the wild because of selection against them.

In *Triticum dicoccoides* and *T. aestivum*, major rDNA loci are found on two pairs of homologous chromosomes, 1B and 6B, which are readily distinguished by the possession of secondary constrictions and by their chromosome-arm length ratios (Appels and Dvorák 1982a). Initial karyotypic analysis of AKL 34 (Matthews 1984) revealed many chromosomes with similar morphology, making it difficult to identify homologous pairs. Whether or not the rDNA loci in AKL 34 are homologous could be addressed directly and perhaps most easily by *in situ* analysis of meiotic cell divisions. Homologous loci would be observed on paired chromosomes during meiotic metaphase I, and heterologous loci would be found on unpaired chromosomes.

To conclude, the structure of taro rDNA, its possible modification by methylation, and its association with nucleoli are consistent with reports for other plant species. Taro *Nor*-locus rDNA does not appear at all unusual, and in later chapters, variation in taro rDNA can be directly related to rDNA variation in other species.

Note

- 1) In later studies (Kokubugata and Konishi 1999, Nakayama et al. 2008), 45S rDNA probes were used for *in situ* hybridisation to chromosomes from taro, and confirmed the presence of two separate rDNA loci in plants with somatic chromosome numbers of $2n=28$. Since the samples involved came from different countries, it is likely that the presence of two loci in the diploid complement of taro is general for the species.

Chapter Thirteen

C. esculenta (Taro) as Homogeneous Taxon

13.1 Hybridisation in the Indo-Malaysian Region?

The name *Colocasia esculenta* (L.) Schott is used today in a broad sense, and refers to a polymorphic species containing many phenotypic varieties, some of which have been given formal descriptions (Plucknett 1983). Little is known about sexual reproduction by Colocasioid genera and species (taxa in Subfamily Colocasioideae) in nature, and it cannot be said how well the existing taxonomy of genera, species, and varieties reflects biological barriers to interbreeding. Hybridisation between biological or taxonomic species has been important in the evolution of many crops, in diverse ways (Simmonds 1976, 1979), and could have contributed to the polymorphism evident in taro today, in theory.

During the present study, it was not difficult to distinguish varieties of taro from other Colocasioid species commonly encountered in the field (notably *Alocasia* spp. and *Xanthosoma sagittifolium*), and from the few available representatives of other *Colocasia* species (*C. affinis*, *C. fallax*, and *C. gigantea*). There was thus no immediate indication of interspecific hybridisation. On the other hand, difficult-to-identify herbarium specimens and mitochondrial DNA polymorphism did suggest the possibility of complex genetic origins.

There are many herbarium specimens of *Colocasia* which collectors, taxonomists, and the present author could not define at the species level, and it is notable that most of these were collected in the Indo-Malaysian region (Appendix 14), where the geographical ranges of the four better known *Colocasia* species overlap (see Chapter Nine, Figure 9.2). Hybridisation between species might therefore account, to some extent, for the difficulty in defining specimens collected there. Other reasons for poor identification include the absence of diagnostic plant parts at the time and place of collection.

Experiments described in Chapter Eleven suggested that the mitochondrial genome of *C. gigantea* is more closely related to that of *Alocasia brisbanensis* than that of *C. esculenta*. This implies that the populations giving rise to the genus *Colocasia* possessed a mixture of different mitochondrial types, or that an *Alocasia* species somehow hybridised with a *Colocasia* species. The latter event seems unlikely, given the major phenotypic differences between genera, but if the suggestion is correct, then there might not be any strong barriers to hybridisation between the phenotypically defined species of *Colocasia*.¹⁾

In this chapter, two kinds of rDNA analysis show that plants identified as taro form

a homogeneous genotypic group that is distinct from other species of *Colocasia* and other Colocasioid genera. A methylatable *Bam* HI site was found in the 18S rRNA gene of all taro varieties tested, and is absent in other taxa. Thermal melting point (T_m) analyses of taro and other taxa show that the large intergenic spacer sequences of different *Colocasia* species have diverged, and that little if any sequence divergence has arisen among varieties of taro, despite the observation of size variation among taro spacer fragments. An apparent interspecific hybrid is identified by T_m analysis, but the general survey of rDNA in taro varieties does not indicate any wider occurrence of hybridisation in the history of taro.

13.2 Materials and Methods

Samples of taro and other species of *Colocasia* were collected and maintained as described in Chapter Ten. Protocols for DNA extraction from young leaves, restriction enzyme digestion, Southern transfer, preparation and hybridisation of radioactive DNA probes, and autoradiography are also given in Chapter Ten. *Bam* HI, *Taq* I, *Hinf* I, and *Rsa* I rDNA fragments were detected using taro rDNA probes prepared from pCe34.1 and pCe34.2, the recombinant plasmids described in Chapter Twelve.

The taxonomic and geographical distributions of a *Bam* HI site near the 3' end of the 18S rRNA gene were examined, and a simple one-step thermal melting protocol (see Chapter Ten) was used for qualitative assessments of similarity between the rDNA spacer sequences of *C. esculenta* var. AKL 34 and other species, varieties, and genera.

For thermal melting point analyses, probes were prepared with either the taro rDNA sequence excised from pCe34.1 or the entire recombinant plasmid. The 5.5 kbp *Eco* RI rDNA fragment in pCe34.1 spans the entire large intergenic spacer, and therefore detected all the variable spacer fragments generated by *Taq* I, *Hinf* I, and *Rsa* I. After hybridisation of the radioactive probe to membrane-bound rDNA fragments at 37°C, a standard low-stringency wash was used to remove weakly bound or unbound probe DNA. The result was recorded by autoradiography, before placing the freshly probed membrane into a hybridising solution at a high temperature such as 66°C. Only probe fragments that were very similar in sequence to target rDNAs were still bound to the filter after the second, high-stringency treatment.

The temperature at which 50% of probe fragments dissociate, for any combination of probe and target DNA, is known as the thermal melting point (T_m). For the second, high-stringency hybridising treatment, a temperature was sought that was near, or at, the T_m of the probe hybridised to itself (i.e., 100% sequence similarity). Visual comparison of the DNA band intensities, before and after the T_m treatment, and allowance for differences in autoradiographic exposure times, allowed an approximate check of the amount of probe actually removed from test samples and a control sample of 100% similarity. High-stringency hybridisation was carried out within one or two days after low-stringency hybridisation, and radioactive decay was therefore negligible because the half-life of the probe isotope, ^{32}P , is two weeks.

Removal of probe by thermal melting is very sensitive to very small differences in

temperature and formamide concentration (Appels and Dvorák 1982a). If too little or too much probe is removed from the control sample of 100% similarity, then the differences in band intensity between these and less similar samples may be too little to detect visually. In some of the experiments summarised here, DNA from AKL 34 was the internal control of 100% similarity, used to assess the effectiveness of the high-stringency wash. No sequence difference was detected in the comparison of AKL 34 and J3A, a wild diploid taro sample from Queensland, and the latter also served as an internal control for some experiments.

13.3 Results

13.3.1 Analysis of Bam HI restriction fragments

The restriction-site map for taro variety AKL 34 (Chapter Twelve) provides a guide for interpreting the *Bam* HI rDNA fragments generated by varieties of taro and by other species and genera in the Tribe Colocasioideae. Of particular interest here are the smaller *Bam* HI fragments from the 18S to 26S rRNA genic region (Figure 13.1). Comparison of these fragments from *C. esculenta* and other Colocasioid species (Figure 13.2) shows that the latter do not possess a *Bam* HI restriction site at the 3' end of the 18S rDNA. To see whether or not this site is diagnostic for *C. esculenta*, *Bam* HI fragments were examined in a wide taxonomic and geographical range of samples. Only *C. esculenta* possesses the 3' 18S site, and it was found in all varieties examined (Table 13.1). In *C. esculenta*, the 2.7 kbp fragments observed are thought to be the result of methylation blocking *Bam* HI cleavage at the 3' 18S site in a proportion of rDNA repeat units. This explanation was noted in Chapter Twelve and is discussed again later. With other Colocasioid species, 2.7 kbp fragments are found, and 1.2 kbp fragments are not found, because there is no *Bam* HI site at the 3' end of 18S rDNA (Figure 13.1).

C. esculenta var. *fontanesii* has a very distinctive phenotype (see Chapter Ten, Figure 10.2), and prior to rDNA analysis, the species identification of this variety was not certain, in the opinion of the present author. The *Bam* HI rDNA fragments generated with this variety (accession T264, result not presented) demonstrated that the methylatable 18S *Bam* HI site is present, consistent with the identification of var. *fontanesii* as a variety of *C. esculenta*. The possibility that some rDNA in var. *fontanesii* is derived from another species is not excluded by the *Bam* HI analysis, but evidence against this possibility is provided by the thermal melting-point analysis described later.

A small range (300 bp) of size variation is evident in the 2.7 kbp *Bam* HI fragments (Figure 13.2), more clearly resolved after shorter exposures than shown here. The differences are probably located in the small intergenic spacers flanking the 5.8S rRNA gene (Figure 13.1). Relatively long exposures are shown here to maximise detection of the 1.2 kbp fragments. The genic region within the taro rDNA probe (pCe34.1) hybridises strongly to the genic 2.7 kbp fragments of Colocasioids of both Australasian origin (*Colocasia*, *Remusatia*, *Alocasia*) and South American origin (*Xanthosoma*, *Caladium*), providing an internal control for detection of the 1.2 kbp fragments.

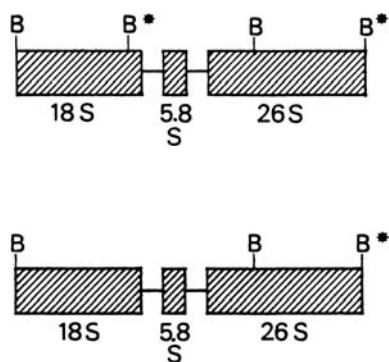


Figure 13.1 *Bam* HI restriction sites in the rDNA genic regions of *C. esculenta* (above) and other members of the Colocasioideae (below). Asterisks mark sites which are consistently not recognised by *Bam* HI in a large proportion of repeat units, probably because of methylation. Small c.1.2 kbp fragments are generated by *Bam* HI cleavage at the 3' end of the 18S rRNA gene (second *Bam* HI site from left). These migrate as one band during electrophoresis, and are diagnostic for *C. esculenta*. When the 3' end of the 18S gene is not cleaved by *Bam* HI, one large fragment of c.2.7 kbp is generated.

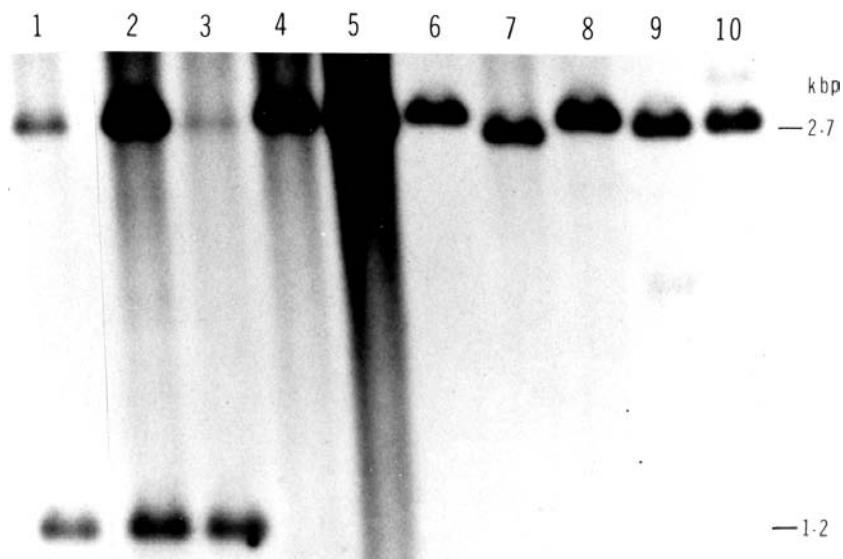


Figure 13.2 A diagnostic test for *C. esculenta* ribosomal DNA. *Bam* HI fragments from the rDNA genic regions of taro and its relatives, detected with the taro rDNA fragment from pCe34.1. Fragments detected include the c.1.2 kbp fragments characteristic of *C. esculenta* and the c.2.7 kbp, 18S-26S genic fragment found in all Colocasioideae tested so far. Restriction-site maps for these fragments are given in Figure 13.1. Samples: 1 = *C. esculenta*; wild, Queensland, Australia (field coll. no. J3A). 2 = T270, putative hybrid (*C. esculenta* x *Colocasia* sp?); ornamental, Australia. 3 = T271, *C. esculenta*; ornamental, Australia. 4 = T328, *C. affinis* var. *jenningsii*; ornamental, Australia. 5 = T259, *C. fallax*; ornamental, Australia. 6 = T268, *C. gigantea*; ornamental, Australia. 7 = T221, *Remusatia vivipara*; wild, Cape York, Australia. 8 = *Alocasia brisbanensis*; wild, Queensland, Australia (field coll. Daly Park N1). 9 = T144, *Xanthosoma saggitifolium*; cultivated, Ifugao, Philippines. 10 = T317, *Caladium* sp.; cultivated, Colombo city, Sri Lanka. All lanes are from the same Southern transfer filter, with an autoradiographic exposure of 53 hours.

Table 13.1 Taxonomic and geographical distribution of the methylatable *Bam* HI site (18S rRNA gene) within Subfamily Colocasioideae. (1) to (3): Numbers of collections tested. The area of origin is indicated in brackets for species known to be collected outside their natural or usual distribution range. (4): The number of different varieties of *C. esculenta* tested was less than 70 because there was replication of varieties among the collections. All 24 Australian collections were of the Jiyer phenotypic variety, from Queensland, and only four phenotypic varieties are represented by the 16 collections from New Zealand. Diploid and triploid taro collections were tested.

(1) <i>Colocasia esculenta</i> (all with methylatable 18S <i>Bam</i> HI site)		
Japan	12	
Philippines	9	
Timor	2	
Papua New Guinea	7	
Australia	24	
New Zealand	16	
(2) <i>Colocasia</i> species (all without the methylatable 18S <i>Bam</i> HI site)		
<i>C. affinis</i>	1	Australia (ex Asia)
<i>C. fallax</i>	1	Australia (ex Asia)
<i>C. gigantea</i>	4	Australia & Asia (ex Asia)
(3) Colocasioid genera (all without the methylatable 18S <i>Bam</i> HI site)		
<i>Alocasia brisbanensis</i>	9	Australia
<i>Alocasia odora</i>	1	Japan
<i>A. cuprea</i> x? (hybrid)	1	Auckland (ex Asia)
<i>A. magnifica</i>	1	Papua New Guinea
<i>Remusatia vivipara</i>	1	Australia
<i>Xanthosoma sagittifolium</i>	1	Philippines (ex South America)
<i>Caladium</i> sp. n.d.	1	Sri Lanka (ex South America)
(4) TOTALS (no. of varieties, species or genera followed by no. of collections, and presence or absence of the methylatable 18S <i>Bam</i> HI site).		
<i>Colocasia esculenta</i> varieties	<70 (70)	present
Other <i>Colocasia</i> species	3 (6)	absent
Other Colocasioid genera	4 (15)	absent

13.3.2 Thermal melting point (T_m) analysis

Temperatures of 66–67°C resulted in the loss by thermal melting of approximately 50% of the taro probe fragments hybridised to taro spacer fragments. The procedure demonstrated clearly that the spacer sequences of *Colocasia* species have differentiated with respect to the spacer sequence of *C. esculenta*, and the result for the putative hybrid T270 confirms that inter-species hybridisation within the genus *Colocasia* is possible (Figure 13.3; plant portrait in Figure 10.6). To determine whether or not such hybridisation has been important in the history of taro, thermal melting point analysis

was used to survey varieties of *C. esculenta* from a range of countries.

A total of thirty-three diploid and triploid taro were surveyed, including plants from Australia, Papua New Guinea, Japan, Madagascar, and Vanuatu (Table 13.2). J3A, an Australian field leaf sample, was from a plant of the Jiyer phenotypic variety (see Figure 10.1), known to be diploid from chromosome counts on plants from the Jiyer and other Queensland sites. It is very likely from previous studies that most of the Papua New Guinea accessions are diploid, and that most of the Japanese accessions are triploid.

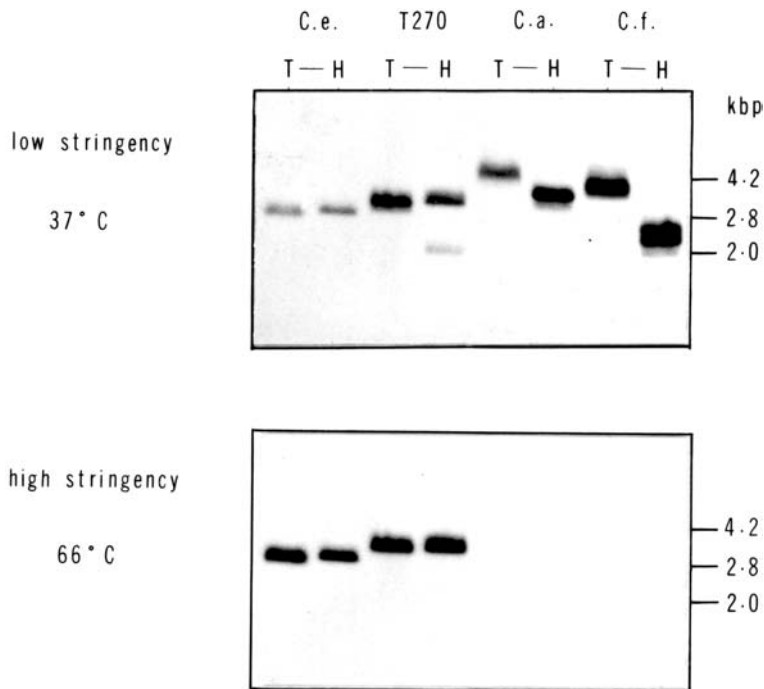


Figure 13.3 Thermal melting point analysis of rDNA spacer sequences in *Colocasia* species. After Southern transfer, *Taq* I (T) and *Hinf* I (H) fragments were probed with the rDNA *Eco* RI fragment from pCe 34.1, which contains an entire large intergenic spacer sequence from *C. esculenta* var. AKL 34. The standard low-stringency hybridisation (30-minute autoradiograph) was followed by a high-stringency treatment (66°C, 150-minute autoradiograph). C.e. = *C. esculenta* (Field coll. J3A, Queensland). T270 = a putative hybrid (*C. esculenta* x another species, possibly *C. affinis*). C.a. = *C. affinis* (T328). C.f. = *C. fallax* (T269).

Sequence similarity between the target spacer fragments of *C. esculenta* (J3A) and the probe from the same species is high, resulting in strong retention of the probe after thermal melting (high-stringency wash). Thermal melting removed probe from the 2.0 kbp *Hinf* I fragments of T270, but not from the larger (3.2 kbp) *Hinf* I fragments, confirming the hybrid origin of this accession. By comparison of the original autoradiographs for each wash of T270, it can be seen that weakly hybridising *Taq* I fragments migrated in the lower part of the c.2.9 kbp *Taq* I band. These fragments may be derived from the same rDNA repeats as the weakly hybridising 2.0 kbp *Hinf* I fragments. Sequence similarity between the probe from *C. esculenta* and the target spacer fragments of *C. affinis* and *C. fallax* is relatively low, resulting in weak retention of probe after thermal melting.

Among twenty-four of the plants surveyed, eight different rDNA spacer fragment patterns were recognised, and clear T_m results were obtained for a further nine collections despite poorly resolved rDNA patterns. The 5.5 kbp *Eco* RI rDNA fragment cloned from AKL 34, and contained in pCe34.1, hybridised as strongly to spacer fragments from other varieties as to the fragments from AKL 34. In other words, no differential loss of probe DNA was observed after sufficient thermal melting to remove approximately 50% of fragments hybridised to rDNA spacer sequences of 100% similarity, as illustrated in Figure 13.4.

Taq I and *Hinf* I spacer fragments from five accessions of *C. esculenta* var. *fontanesii* were also tested, using pCe34.1 and a thermal melting temperature of 67°C. As suggested above, the species identification of this variety was questionable. Each accession tested (T 264, 291, 330, 339, and 322) displayed the same pattern of rDNA spacer fragments (see Chapter Fourteen, Figure 14.11), and none of the fragments

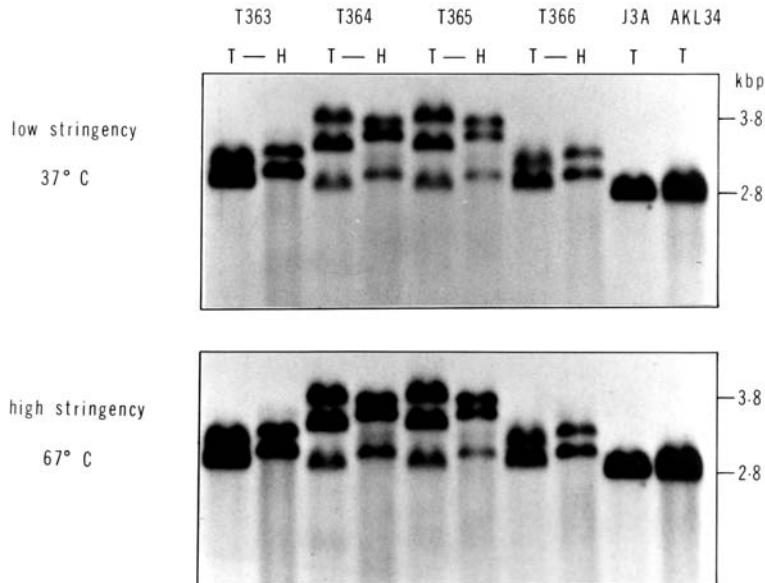


Figure 13.4 Thermal melting point analysis of rDNA spacer sequences in varieties of *C. esculenta*. After Southern transfer, *Taq* I (T) and *Hinf* I (H) fragments were probed with the rDNA *Eco* RI fragment from pCe34.1, which contains an entire large intergenic spacer sequence from *C. esculenta* var. AKL 34. The standard low-stringency hybridisation (3-hour autoradiograph) was followed by a high-stringency treatment (67°C, 6-hour autoradiograph). T363 to T366 are cultivars from Madagascar, J3A is a wild variety from Queensland, Australia, and AKL 34 is a cultivar from New Zealand.

The analysis of AKL 34 with its derivative pCe34.1 displays approximately 50% thermal melt-off under the condition of 100% sequence similarity between probe and target DNA. The second autoradiographic exposure was twice as long as the first, but gave rDNA bands of similar intensity, thus indicating that a 50% thermal melt-off was achieved. Retention of the probe by spacer fragments appears equally strong for J3A, and T363 to T366. Similar results from thermal melting point analysis were obtained for a wide range of taro samples (see Table 13.2).

Table 13.2 List of plants tested for thermal melting point analysis of rDNA spacer sequences in *C. esculenta*. Spacer fragments were generated with *Taq* I, *Hinf* I, or *Rsa* I, before Southern transfer and probing as illustrated in Figure 13.4. For each country from which plants were obtained, the classes of rDNA patterns are noted (Qld 1:1, Puk 1:2, etc; A-C: described in Chapter Fourteen) followed by the field or accession (T) numbers, and chromosome numbers if known.

Australia (n = 1, <i>Taq</i> I, <i>Hinf</i> I)	
Qld 1:1	J3A (2n= 28)
Papua New Guinea (n = 13, <i>Taq</i> I, <i>Hinf</i> I)	
Qld 1:1	T247, 258
Puk 1:2	T197, 198, 202, 205, 208
Buk 2:1	T203
Puk 2:3	T188, 190, 193
Not determined	T206, 207
Japan (n = 11, <i>Rsa</i> I)	
A	T294, 305
B	T296, 303
C	T298, 299 (2n = 42), 302 (2n = 42), 306
Not determined	T293 (2n = 42), 304, 326
Madagascar (n = 4, <i>Taq</i> I, <i>Hinf</i> I)	
Puk 2:3	T363, 366
Col 3:4	T364, 365
Vanuatu (n = 4, <i>Taq</i> I, <i>Hinf</i> I)	
Not determined	T377, 378, 379, 380

showed any lack of sequence similarity when the probe from *C. esculenta* var. AKL 34 was removed by thermal melting (data not shown). This supports the identification of var. *fontanesii* as a variety of *C. esculenta*, and suggests that no other species has contributed to the rDNA complement, assuming that differentiation among all *Colocasia* species is accompanied by a degree of rDNA differentiation similar to that seen in the comparison of *C. esculenta*, *C. affinis*, and *C. fallax*.²⁾

13.4 Concluding Discussion

Restriction site analysis of the 18S rRNA gene and thermal melting point analysis of the intergenic spacer region both indicate that *C. esculenta* is a homogeneous taxon, distinct from other species of *Colocasia*. Heterologous-probe analysis of mitochondrial DNA (Chapter Eleven) led to the same conclusion. The history of taro may therefore simply be the history of one species evolving in Asia and then gaining an extended distribution by natural dispersal and with the assistance of humans. There is no evidence that polymorphism within this species was generated by interspecific hybridisation. In the chapter that follows, differentiation within the species *C. esculenta* is illustrated by a

survey of variation attributed to length mutation in large intergenic spacers of rDNA.

Because the sequence of the 18S gene, methylatable *Bam* HI site is in a conserved region of rDNA, it is expected that a similar sequence exists in other species of *Colocasia*. As there are no sequence data for these, an inspection was made of 18S gene sequences published for distantly related plant taxa. Near the 3' end of the 18S gene in rice, in a position that corresponds to the approximate map position of the taro *Bam* HI site, a nine-base pair sequence was found which matches the eight-base sequence predicted for taro (Figure 13.5). The taro sequence is predicted by assuming that methylation of the six-base *Bam* HI site occurs and requires the presence of flanking cytosine and guanosine residues, as suggested in Chapter Twelve. Dams et al. (1988) aligned the 18S sequences of diverse plant and animal taxa. The sequence for rice (Figure 13.5) may be regarded as a latent methylatable *Bam* HI site, in that loss of one guanosine residue would be sufficient to create the required sequence. It is proposed here that the *Bam* HI site in taro is a phylogenetically derived character state, since it is absent from other species of *Colocasia*, and from other genera such as *Xanthosoma* and *Caladium*, which are definitely phylogenetic outgroups. Latent *Bam* HI sites among near relatives of taro probably differ from the rice sequence, and the specific mutational event that gave rise to the *Bam* HI site in taro cannot be determined by comparison to rice.

Comparison of the aligned sequences for distantly related plant taxa (Figure 13.5) suggests a local hot spot of variability just where it is proposed that a single base deletion would transform the rice sequence into a *Bam* HI site. By analogy to the kinds of variability exhibited by the aligned sequences, it is proposed that the *Bam* HI site in *C. esculenta* arose by base substitution and/or deletion.

Of interest for future investigation is the slight size variation apparent among the 2.7 kbp *Bam* HI fragments from different species of *Colocasia* and different *Colocasioid* genera (Figure 13.2). The 2.7 kbp fragment spans the two small intergenic spacers and the 5.8S gene, between the 18S and 26S genes (Figure 13.1), a region which has been found by thermal melting analysis to vary in sequence among species of *Triticum* (Appels and Dvořák 1982b; see Chapter Nine, Figure 9.5). This region has not been intensively studied in plants, but a comparison of sequences in two species of toad (Furlong and Maden 1983) and a phylogenetic study of frog species (Hillis and Davis 1986) have shown that interspecific variation in the two small (transcribed) spacers involves insertions, deletions, and base substitutions.

The presence of a species-specific *Bam* HI site in the 18S gene provides a potentially useful target for species diagnosis of archaeological DNA residues using the polymerase chain reaction (PCR). PCR is currently regarded as an ideal tool to amplify very small numbers of, or even single, intact ancient DNA molecules present in a vast excess of damaged molecules (Pääbo et al. 1989). Because archaeological DNA residues will be highly degraded, if found, it is necessary for diagnostic characters to be located within very short sequences. More detailed analysis of the sequences immediately flanking the methylatable 18S *Bam* HI site might reveal other diagnostic features. These would make false identifications due to evolutionary convergence or technical artefacts less likely, should the PCR technique be employed in the future.

Species													
C. e.			<u>C</u>	G	G	A	T	C	-	C	<u>G</u>		
O. s.	T	T	<u>C</u>	G	G	A	T	C	G	C	<u>G</u>	G	C
Z. m.	T	T	<u>C</u>	G	G	A	G	C	T	C	<u>G</u>	G	C
G. m.	T	T	<u>C</u>	G	G	A	T	T	G	C	<u>G</u>	G	C
C. r.	T	T	<u>C</u>	G	G	A	T	T	G	-	A	G	C

Figure 13.5 The methylatable *Bam* HI site from the 18S rRNA gene of taro, aligned with 18S rDNA sequences published for other plant taxa. C.e. = *Colocasia esculenta* (taro), O.s. = *Oryza sativa* (rice), Z.m. = *Zea mays* (corn), G.m. = *Glycine max* (soybean), C.r. = *Chlamydomonas reinhardtii* (a green alga). Deletion of one guanosine residue (G) from a sequence like that reported for rice would create a methylatable *Bam* HI site like that predicted for taro. Conserved bases in the published sequences, relative to rice, are boxed. The recognition sequence for *Bam* HI, GGATCC, is in bold type; underlining marks bases which are required for cytosine methylation in the sequences shown, or their complements. The sequence for rice begins 105 base pairs from the 3' end of the 18S rRNA gene, and at base position 3443 in the alignment for rice and other species compiled by Dams et al. (1988). Homology between the 12–13 bp sequences illustrated for rice, corn, soybean, and *Chlamydomonas* was established by aligning complete, approximately 1800 bp, 18S rDNA sequences (ibid).

Thermal melting analysis demonstrates that differences in the sizes of rDNA spacer fragments, within and between varieties, are not associated with major changes in sequence content (Figure 13.4). In Table 13.2, the rDNA classifications of the tested accessions represent different combinations of variously sized rDNA spacer fragments. These observations are consistent with the suggestion (Chapter Twelve, Figure 12.3) that spacer fragments from taro vary in size according to the copy number of a short repeated sequence (sub-repeat) within each spacer. The inferred sub-repeat sequence of taro varies little among rDNA variants and phenotypic varieties.

Sequence divergence among the rDNA spacers of *Colocasia* species is recorded in Figure 13.3. Exact thermal melting points for hybridisation of the taro probe to taro and other species were not determined, so the amount of sequence differentiation between species cannot be quantified. For a comparison of *Triticum* species, using *Triticum* probes, Gill and Appels (1988) regularly used high-stringency temperatures of 63–64°C, equal or close to the T_m of the 130 bp spacer sub-repeat from *T. aestivum* cv Chinese Spring, hybridised to rDNA of the same variety (Appels and Dvořák 1982a). T_m analysis for *Colocasia* was conducted without prior knowledge of the degree of differentiation between species, or of the T_m for the taro probe hybridised to taro rDNA, but the choice of temperature was guided by the previous T_m analysis of rDNA spacer sequences in wheat. Relatively high temperatures, compared to those used for wheat, were chosen to ensure that thermal melting would be observed. The internal controls (probe and target

DNA the same or very similar) indicated that temperatures of 66°C and 67°C were close to the T_m for taro DNA-taro DNA hybridisation. The exact temperatures realised in experiments set at 66–68°C may have differed by as much as plus or minus 0.5°C. In some experiments set at 67°C, and in one of 68°C, much more than 50% of the taro probe was removed from taro rDNA, and the results could not be relied upon to provide any discrimination between taro varieties. For maximal differentiation between *Colocasia* varieties and species, a high-stringency temperature less than 67°C is probably needed.

The hybrid variety T270 is phenotypically similar to *C. affinis* var. *jenningsii* in that it possesses decorative patches of anthocyanin between the secondary veins of the leaf blades (compare Figure 10.5 and 10.6, Chapter Ten), but under the conditions of maintenance in Canberra its growth is more vigorous, similar to that of *C. esculenta*. In Canberra, *C. affinis* var. *jenningsii* grows weakly in the glasshouse and loses its leaves during winter. Engler and Krause (1920: 68) described *C. marchallii* Engler as a possible hybrid of *C. affinis* and *C. antiquorum* (= *esculenta*), and noted that it is cultivated in glasshouses (in Europe) and that its origin is unknown. T270 and *C. marchallii* resemble each other in leaf shape and coloration, but a full comparison with the description by Engler and Krause (1920) is not possible because a complete inflorescence was not obtained from T270.

Assuming that T270 is a hybrid formed by *C. affinis* (variety not specified) and *C. esculenta*, then it might be a product of natural hybridisation within the relatively limited range recorded for *C. affinis* (Northeast India to Burma, including Northwest Thailand, see Chapter Nine, Figure 9.2). This is the same area in which most collections of indeterminate species identity have been collected. T270 is stoloniferous, and in the potted condition does not produce a starchy corm. This and other hybrids may have arisen naturally in the Indo-Malayasian region without generating varieties favoured by humans for cultivation and/or dispersal in the wild, as food plants. With the exception of T270, the rDNA analyses do not suggest that interspecific hybridisation has occurred, but other genotypic components from other species could have introgressed into populations of *C. esculenta*.

Alternatively, hybridisation between *Colocasia* species might require human intervention, for reasons beyond the scope of the present discussion. *C. affinis* var. *jenningsii* is widely, though not commonly, cultivated in glasshouses (Engler and Krause 1920; present author, personal observation). Although regarded by Engler and Krause (1920) as originating in tropical Himalaya, no definitely wild specimens of var. *jenningsii* have been located in European herbaria by the present author. If var. *jenningsii* is not of natural origin, and is a parent of T270 (= *C. marchallii*?), then T270 is certainly not a natural hybrid.

Notes

- 1) Experimentally, it has been shown that intergeneric crosses with *Colocasia* are possible, though the resulting offspring are sterile (see references cited in Ahmed et al. 2013). Ahmed (pers. comm. 2013) has found evidence of hybridisation between *C. esculenta* and wild *Colocasia*

species found in northern Vietnam. Analysis of chloroplast DNA sequences suggests that *C. gigantea* should be regarded as a separate genus, more closely related to *Alocasia* than *Colocasia* (Ahmed et al. 2013; Figure 2c).

- 2) *C. esculenta* var *fontanesii* (accession T322 from Sri Lanka) is shown in Figure 10.2. In recent years, numerous new species of *Colocasia* have been described in Southeast Asia (see Chapter 18).

Chapter Fourteen

Nor-Locus rDNA Variation in C. esculenta

14.1 Introduction

Ribosomal DNA was surveyed in a wide range of wild and cultivated taro from Asia and the Pacific. When taro DNA was digested with the restriction enzymes *Taq* I, *Hinf* I, and *Rsa* I, highly polymorphic fragments from the large intergenic spacer region of rDNA repeat units were generated. The fragments varied in their length (number of nucleotide base pairs) and were used to create an rDNA typology for taro. Many of the polymorphisms were correlated with differences in the overall length of rDNA repeat units. This indicates mutations involving insertions or deletions of nucleotide sequences, rather than single nucleotide substitutions in the recognition sequences of restriction enzymes used for analysis (an individual base substitution can cause a recognition site gain or site loss). The latter kind of mutation probably also contributed to the observed range of rDNA variants. The mutational events that caused variation in taro rDNA were not the immediate object of investigation, and remain largely unresolved. Analogy with rDNA variation studied in other taxa suggests that most rDNA variation in taro is related to increases or decreases in the number of sub-repeat sequences (a form of sequence insertion and deletion mutation) within the large intergenic spacer regions of rDNA repeats.

The analyses outlined above did not provide absolute measures of parentage or identity among individual plants, varieties, or vegetatively propagated lineages. Different mutational events, and reassortment of chromosomes during sexual reproduction in different locations, could have produced similar overall patterns of rDNA variants in different locations. *Taq* I and *Hinf* I analyses were conducted to establish a typology of rDNA variation. The ribosomal DNA patterns of wild and cultivated taro from different areas are compared in terms of this typology.

In the survey, the simplest rDNA pattern found was one that represented a single rDNA variant (Qld 1:1 class in the typology of *Taq* I and *Hinf* I restriction fragment patterns). This was the only variant found in wild taro over 400 km of the wet tropical rain forest zone of northeastern Queensland. The Queensland rDNA variant appears to be present in other wild populations in Australia and Papua New Guinea, and in cultivated taro from Asia, Papua New Guinea, and the Pacific Islands. Individual plants from wild populations in Australia (not including Queensland) and Papua New Guinea, and many plants from cultivations outside Australia, display mixtures of rDNA variants. Genotypic heterogeneity was detected among diploids and triploids, suggesting diverse origins (as sexual progeny) for the clonal lineages within each cytological group. A comparison of

phenotypic and rDNA variation suggests that the often-noted phenotypic diversity of cultivated taro is inversely related to genotypic diversity, as measured by rDNA analysis. This is thought to reflect positive selection by humans for variability in the colour characters used to measure phenotypic diversity.

Ribosomal DNA variation among a small number of Japanese triploid varieties is correlated with the previous classification of those varieties by Japanese botanists based on phenotypic characters. The temperate adapted Japanese cultivars lack the Queensland rDNA variant, which appears widespread elsewhere. The rDNA patterns displayed by the New Zealand triploid varieties RR and GR were identical (see also Chapter Ten), and were similar to those of the Japanese triploid taro group *Eguimo*, thought by Japanese botanists to have originated in China.

Cultivated taro from Madagascar, the Philippines, Papua New Guinea, Tonga, and the Society Islands shared a pattern of rDNA fragments identified in the typology as the Puk 2:3 class. The Col 3:4 class was found in taro accessions from Madagascar, Sri Lanka, and Japan. Both these classes represent mixtures of rDNA variants found within individual plants. Assuming that the shared rDNA patterns are in some sense monophyletic (of one origin, each rDNA variant individually or as a mixture of variants), then some kind of historical connection is suggested for very widely distributed lineages of cultivated taro. For each rDNA class, it is not known whether the combination of rDNA variants originated in one location, or whether it originated independently in many different locations from a widely distributed set of similar wild progenitors. For the New Zealand triploids, and for an ornamental triploid variety, var. *fontanesii*, historical records provide a basis for suggesting recent transfers between specific geographical areas.

The ribosomal DNAs of phenotypically similar wild taro in different regions of northern Australia and in Papua New Guinea are different. Within northern Australia, different rDNA classes are distributed homogeneously within different areas, demonstrating the existence of limits to past dispersal of taro within Australia by humans and by natural means.

14.2 Materials and Methods

Plants were collected and maintained as described in Chapter Ten. DNA extracts were prepared from fresh leaves or leaves stored in liquid nitrogen and analysed using the protocols described in Chapter Ten for restriction endonuclease digestion, agarose gel electrophoresis, Southern transfer to nylon filters, hybridisation with radioactive rDNA probes, and autoradiography. All probes were made as described in Chapter Ten using the taro rDNA clones described in Chapter Twelve. The clone pCe34.1 contains an approximately 5.5 kbp *Eco* RI fragment which spans the large intergenic spacer (IGS) region, from the 3' end of the 26S gene to near the 3' end of the 18S gene. The clone pCe34.2 contains an approximately 4 kbp *Eco* RI fragment which spans the genic regions from near the 3' end of the 18S gene, to near the 3' end of the 26S gene. pCe34.11 contains a subcloned 2.8 kbp *Taq* I fragment from the IGS region within pCe34.1, provided IGS-specific probes. The recombinant plasmids (vector plus insert) were either

used as probes directly, or as sources for purified rDNA inserts, which were also used as probes.

Size estimates, for fragments detected by autoradiography, were made by calibration with standard size markers as described in Chapter Ten. In addition, an internal control for experimental variation between gels was used, in the survey of *Taq* I and *Hinf* I restriction fragments, as follows. A standard sample was included with each set of test samples. This sample was a digest of total DNA from one plant (J3A) harvested in Queensland at the Jiyer Cave site. J3A gave one size of rDNA fragment when digested with either *Taq* I or *Hinf* I. Best estimates for these fragments were calculated as the mean of several independent estimates, i.e., separate gels. The mean for *Taq* I was 2779 bp, with a standard deviation (n-1) of 114 bp, based on 14 tests, and the mean for *Hinf* I was 2865 bp, with a standard deviation (n-1) of 118 bp, based on 7 tests. One or the other of these means was used to calculate a correction factor for each test gel: correction factor = mean/control. The previously obtained estimate for each autoradiograph band was multiplied by the correction factor, which was generally close to one.

All accessions tested with *Taq* I and *Hinf* I are listed in Appendix 20, with general location, habitat, chromosome number if known, and rDNA class if known.

14.3 Results

14.3.1 Spacer fragment variation within taro generally

Figure 14.1 summarises intergenic spacer variation detected in *C. esculenta* after *Taq* I and *Hinf* I analysis. Spacer fragment sizes represented by individual autoradiograph bands were estimated for all individuals, after normal autoradiographic exposure; that is, long enough for resolution of the major bands. The results for cultivated and wild taro, from Asia and the Pacific, are summarised in Table 14.1 for *Taq* I analysis and in Table 14.2 for *Hinf* I analysis. The variety *C. esculenta* var. *fontanesii* was not included in these summaries because its recorded distribution is largely due to historically recent dispersal as an ornamental (see below). For convenience, four Madagascan samples were included in the present summaries as Asian, because Madagascar was colonised by Asians by at least several hundred years ago (Battistini and Verin 1972, Bellwood 1985), and the plants almost certainly came from Asia.

The differences detected by *Taq* I and *Hinf* I are highly correlated because these enzymes cut DNA on each side of the same variable region within the large intergenic spacer (see Chapter Twelve). Figure 14.2 illustrates the correlation between differences among *Bam* HI and *Eco* RI fragments, which span the entire IGS region, and differences between fragments generated by *Taq* I and *Hinf* I. The correlations indicate that the restriction fragment polymorphisms are due to a length difference within the intergenic spacer region. Additional 2 kbp fragments generated by *Taq* I analysis of T294 are not associated with differences among the large *Bam* HI and *Eco* RI fragments, nor with differences among the *Hinf* I fragments, and indicate the presence of minor class (low copy number) of repeat units. The 2 kbp fragments presumably reflect some other kind of mutation, probably either an inversion or a base substitution.

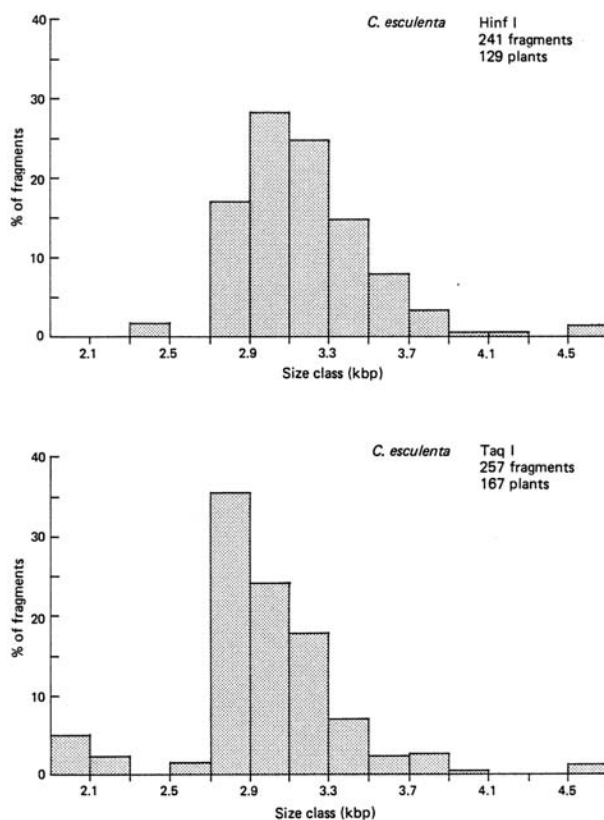


Figure 14.1 Percentage frequencies of *Taq* I and *Hinf* I rDNA intergenic spacer fragments in different size classes. Using *Taq* I, 257 fragments were detected in 167 plants (data from Table 14.1); using *Hinf* I, 241 fragments were detected in 129 plants (data from Table 14.2).

A provisional typology of rDNA spacer fragment patterns is advanced in Table 14.3. The mean size estimates for fragments in each class were not based on fully independent estimates for individual collections, since samples belonging to one class frequently occurred more than once on the same Southern filter, and were therefore subject to the same sources of estimation error. The essential defining criterion for admission to each class was the range of fragment sizes exhibited, rather than the intensity of bands containing the fragments. Band intensities were usually but not always consistent among the patterns assigned to the same class. The assignment of an rDNA pattern to an already recognised class was often based on a single test with each enzyme. Samples for which digests with *Taq* I and *Hinf* I were not electrophoresed on the same gel were not classified (except in the case of Queensland samples with single *Taq* I and *Hinf* I bands) because the relative positions of multiple *Taq* I and/or *Hinf* I bands were also assessed visually to confirm the similarity of restriction fragment patterns. The geographical

Table 14.1 Frequency distributions for rDNA spacer fragment size variants, detected after *Taq* I analysis of wild and cultivated taro from Asia, Papua New Guinea, Australia, and the Pacific Islands. The numbers of assays (plants used) for each area, and each habitat, are shown below, and the sum frequencies for fragment size variants are shown at right. On average, 1.5 different fragments (size variants) were detected per plant (257 fragments/ 167 plants).

Size class kbp	Asia		P.N.G.		Australia		Pacific Is.		Sum Fragments		All	%
	Cult	Wild	Cult	Wild	Cult	Wild	Cult	Wild	Cult	Wild		
1.9 - 2.09	8		1			4			9	4	13	5.0
2.1 - 2.29	2		2			2			4	2	6	2.3
2.3 - 2.49												
2.5 - 2.69	1		2				1		4		4	1.6
2.7 - 2.89	11	1	24	2		29	19	5	54	37	91	35.4
2.9 - 3.09	17	1	23	5		14	2		42	20	62	24.1
3.1 - 3.29	22	3	10	1			6	4	38	8	46	17.9
3.3 - 3.49	7	2	3			2		4	10	8	18	7.0
3.5 - 3.69	3		1			2			4	2	6	2.3
3.7 - 3.89	3	2	2						5	2	7	2.7
3.9 - 4.09	1								1		1	0.4
4.1 - 4.29												
4.3 - 4.49												
4.5 - 4.69				3						3	3	1.2
Sum Assays	33	4	50	6	0	44	21	9	104	63	167	

Table 14.2 Frequency distributions for rDNA spacer fragment size variants, detected after *Hinf* I analysis of wild and cultivated taro from Asia, Papua New Guinea, Australia, and the Pacific Islands. The numbers of assays (plants used) for each area, and each habitat, are shown below, and the sum frequencies for fragment size variants are shown at right. On average, 1.9 different fragments (size variants) were detected per plant (241 fragments/129 plants).

Size class kbp	Asia		P.N.G.		Australia		Pacific Is.		Sum Fragments		All	%
	Cult	Wild	Cult	Wild	Cult	Wild	Cult	Wild	Cult	Wild		
1.9 - 2.09												
2.1 - 2.29												
2.3 - 2.49						4				4	4	1.7
2.5 - 2.69												
2.7 - 2.89	11		15	3		3	8	1	34	7	41	17.0
2.9 - 3.09	9	1	27	5		17	9		45	23	68	28.2
3.1 - 3.29	27	2	22	3		1	5		54	6	60	24.9
3.3 - 3.49	16	3	12	3			2		30	6	36	14.9
3.5 - 3.69	7	3	6			2	1		14	5	19	7.9
3.7 - 3.89	6		1			1			7	1	8	3.3
3.9 - 4.09			1						1		1	0.4
4.1 - 4.29	1								1		1	0.4
4.3 - 4.49												
4.5 - 4.69				3						3	3	1.2
Sum Assays	36	4	46	6	0	21	15	1	97	32	129	

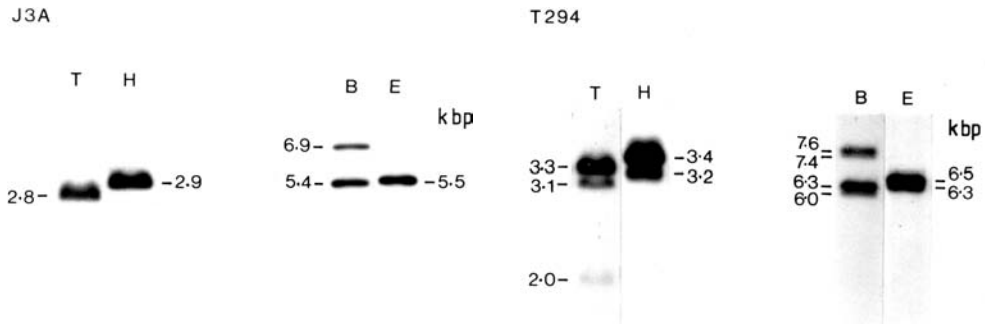


Figure 14.2 Contrasting examples that illustrate rDNA length variation within and between plants. The interpretations are guided by reference to Figures 12.2 and 12.4. The sample J3A produces single *Taq* I and *Hinf* I rDNA fragments, which span overlapping portions of the large intergenic spacer region. The combined pattern of *Taq* I and *Hinf* I fragments is identified as the Qld 1:1 class. The much larger *Bam* HI and *Eco* RI fragments, which span the entire spacer region, are also single, and J3A thus appears to contain a single rDNA length variant. This variant is shorter, in kilobasepairs, than the variants displayed by T294.

The *Taq* I and *Hinf* I spacer fragments from T294 form doublets with separations of approximately 200 bp, and doublets which reflect similar size differences are evident among the larger *Bam* HI and *Eco* RI fragments. The doublets are most simply attributed to one 200 bp length difference within the spacer region, rather than to independent losses or gains of *Taq* I, *Hinf* I, *Bam* HI, or *Eco* RI restriction sites. Although the origin of the faint 2.0 kbp spacer fragment is not yet known, length mutation does not appear to be involved.

J3A is a wild diploid variety (Jiyer phenotype) from Jiyer Cave, Russell River, Queensland; T294 is a cultivated triploid variety (Shōgaimo phenotype group) from Tokushima, Japan.

distributions recorded for each rDNA class are summarised in Table 14.4. The integrity of the Puk 1:2 class is dubious. Replicate tests of Queensland-type rDNAs with *Hinf* I frequently generated a partial digestion product resembling the upper, low intensity *Hinf* I band recorded for the Puk 1:2 class. The numbers of individuals possessing only the Queensland rDNA variant, in Table 14.4, have probably been underestimated.

14.3.2 Wild taro in Australia and Papua New Guinea

Samples from coastal northeastern Queensland were collected over the entire recorded range of the Jiyer wild phenotype, between Ingham and the Endeavour River, a distance of approximately 400 km (Figure 14.3; for phenotype see Figure 10.1). Chromosome counts of $2n = 28$ were obtained for three sites, from north to south: (5) Hope Vale; (10) Russell River; (8) Blues patch (Figure 14.3).

Twelve plants from sites 1 to 4, and one plant from site 13, were tested with *Hinf* I, and 35 plants from sites 1 to 13 were tested with *Taq* I (Figure 14.4). In replicated tests with the plant J3A (field number) from Jiyer Cave (site 10), *Taq* I and *Hinf* I digests were electrophoresed together, establishing the Qld 1:1 rDNA class (Table 14.3 Figure 14.2). In replicated tests with *Hinf* I and one DNA extract from J3A, a faint, upper *Hinf* I band was frequently but not always detected, indicating partial digestion. The faint, upper *Hinf* I bands in Figure 14.4 (sites 1 to 4) reflect the same partial digestion effect. The

Table 14.4 General geographical distributions of rDNA classes identified in 86 samples of cultivated and wild taro (including the Eli 3:5 class of var. *fontanesii*).

r DNA class	Asia		PNG		Australia		E. Pacific		Total
	Cult	Wild	Cult	Wild	Cult	Wild	Cult	Wild	
Qld 1:1			4			14	4		22
Puk 1:2			18				1		19
East 1:3							2		2
Buk 2:1			1						1
Arn 2:2						4			4
Kim 2:2						3			3
Bay 2:2	2								2
Col 2:2		1							1
Moro 2:2				1					1
Moro 2:3A				1					1
Moro 2:3B				1					1
Puk 2:3	3		6	1			2		12
Kat 2:3	1								1
Min 3:2	2								2
Ruti 3:2A			1						1
Ruti 3:2B			2						2
Moro 3:3				1					1
Col 3:4	3	1							4
Eli 3:5		1			3		1		5
Kat 4:4	1								1

absence of variation among the rDNAs of Queensland wild taro was further confirmed by analysis with *Rsa* I (31 samples from sites 1 to 12), *Bam* HI (34 samples from sites 1 to 12), and *Eco* RI (21 samples from sites 5 to 12).

For sampling within a site, samples were taken from physically separate shoots distantly located from each other within the site. This maximised the chance of detecting variation among sexual progeny (clones derived from different seed), and minimised the chance of collecting identical material from just one clone. The success of this strategy could not be measured because different clones could not be identified in the field. Despite the deliberate attempt to maximise the detection of variation, none was found over the entire range surveyed. At the time of sample collection (September and October 1987) flowering was recorded at sites 4, 7, and 10, and fruit with seed were found at site 5 (Hope Vale Mission), so taro probably do reproduce by seed in Queensland (see also Figure 9.3).

Live collections of wild taro from Kimberley and Arnhem Land, in northern

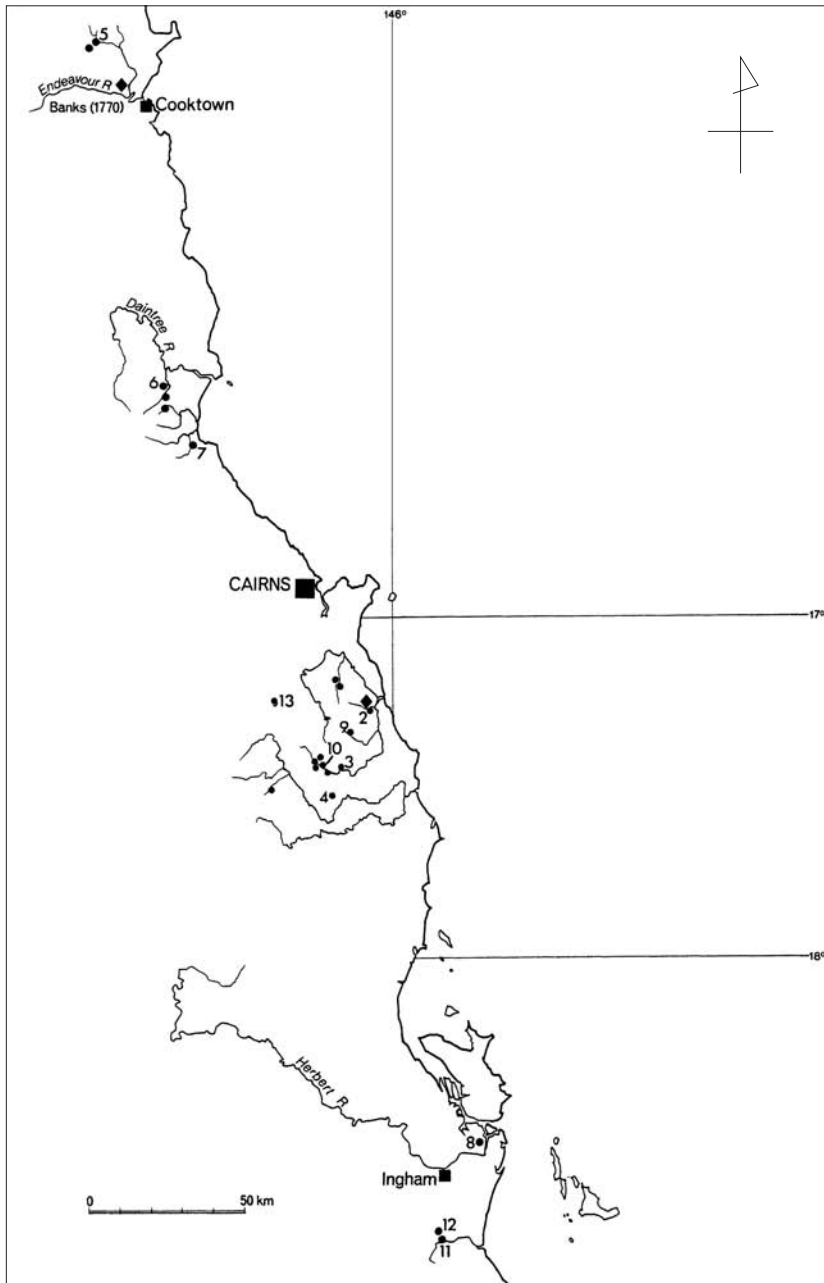


Figure 14.3 Locations of wild taro of the Jiyer phenotype (Figure 10.1) recorded in Queensland in 1987–88. The numbered sites are those for which rDNA analyses were carried out: (1) Whyanbeel Creek; (2) Harvey Creek, Bellenden Ker; (3) Combos Crossing, Russell River; (4) Badgery Creek, Johnstone River; (5) Hope Vale, Endeavour River; (6) Cassowary Creek, Daintree; (7) South Mossman River; (8) Blues patch, Herbert River; (9) Boulder Falls, Bellenden Ker; (10) Jiyer Cave, Russell River; (11) Gap Creek, Halifax Bay; (12) Gin Creek, Halifax Bay; (13) Lake Barrine, Atherton Tableland.

Australia, were received and tested with *Taq* I and *Hinf* I (Figure 14.5). Two further classes of rDNA pattern were recognised; Kim 2:2 from the Kimberley, and Arn 2:2 from Arnhem Land (Figure 14.5). Tests similar to those illustrated in Figure 14.5 were performed with *Taq* I and/or *Hinf* I, and with pCe34.1 or pCe34.11 as probes, for one plant per site from four sites in Kimberley (T335, 336, 337, and 386), and a total of six plants from five sites in Arnhem Land and the western coast of the Gulf of Carpentaria (T31, 331, 332, 333, 338, 376). Although *Taq* I and *Hinf* I fragments were not observed for every Kimberley and Arnhem Land sample, each restriction enzyme alone appears

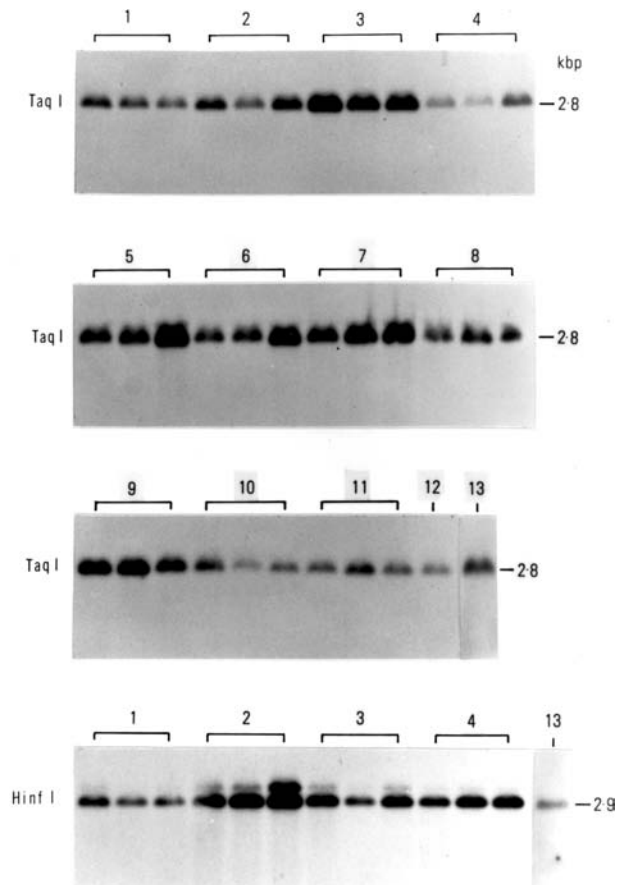


Figure 14.4 Ribosomal DNA analysis of wild taro in Queensland, Australia, sites 1–13 (see Figure 14.3). *Taq* I and *Hinf* I spacer fragments detected in autoradiographs after Southern transfer and probing with pCe34.1.

The results for *Taq* I are compiled from four radiographs, one for each group of sites: sites 1–4 (uppermost set), sites 5–8, sites 9–12, and site 13. The results for *Hinf* I (lowermost set) are compiled from two autoradiographs, one for sites 1–4 and one for site 13. The faint upper band observed with *Hinf* I is believed to be a partial digestion product.

diagnostic for the different rDNA classes within Australia. The ribosomal DNA patterns observed are homogeneously distributed in Kimberley and Arnhem Land, as well as in the more thoroughly surveyed Queensland area. The sample T376 (Gulf of Carpentaria) produced an rDNA pattern classified as Arn 2:2, according to the spacer-fragment size range, although the autoradiograph band intensities were not the same as for the Arnhem Land samples (result not presented).

Under potted conditions in Canberra, the plants from Kimberley and Arnhem Land were phenotypically very similar to the Queensland wild-type (Figure 10.1), though

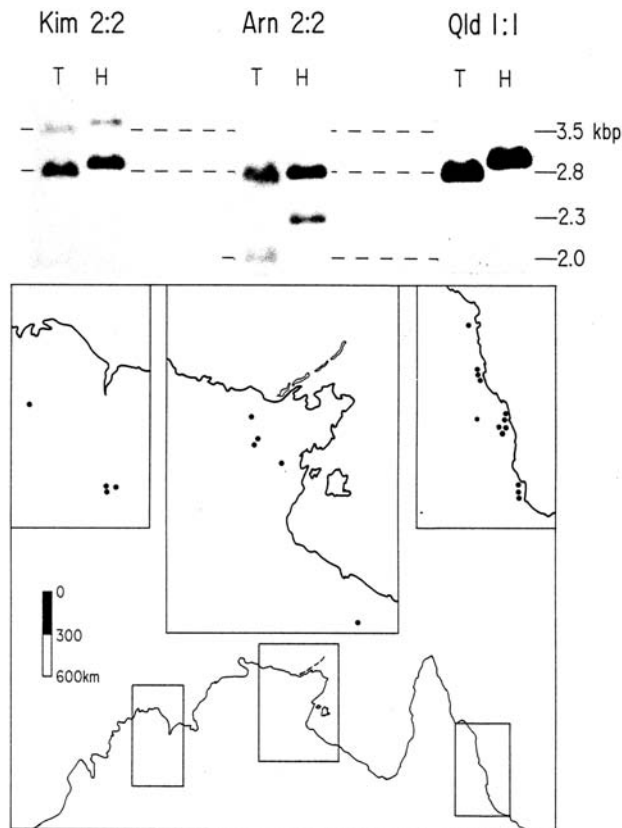


Figure 14.5 Ribosomal DNA in Australian wild taro. Upper panel: three different patterns of *Taq* I and *Hinf* I spacer fragments (classes Kim 2:2, Arn 2:2, Qld 1:1), detected in an autoradiograph of one filter after Southern transfer and hybridisation-probe analysis with pCe34.1. The three samples, left to right, are T336 (vic. Drysdale River, northern Kimberley, coll. S. Forbes 1984), T31 (vic. Maningrida, northeastern Arnhem Land, coll. R. Jones 1980), and J3A (Jiyer Cave, Russell River, northeastern Queensland, coll. P. Matthews 1987).

Lower panel: locations of all samples tested with *Taq* I and/or *Hinf* I. The plants in each region displayed rDNA spacer fragments characteristic for the rDNA patterns illustrated directly above, indicating regional homogeneity in the distribution of rDNA variation.

leaves from one Kimberley plant exhibited a small amount of red anthocyanin pigmentation, at the junction of the petiole and the blade. The Kimberley and Arnhem Land populations are identified here, provisionally, as possessing the Jiyer phenotype. Detailed phenotypic records were made during the Queensland field trip (dimensions of leaves and inflorescences) and it is hoped that similar observations can be made in northern Australia in the future.

The Kimberley rDNA spacer fragments are not extreme in terms of size, but exist in a combination not found elsewhere within or beyond Australia (Table 14.4). The Arnhem Land rDNA pattern (Arn 2:2) includes *Hinf* I fragments of 2.3 kbp, the smallest recorded for taro, and the recorded distribution of the Arn 2:2 pattern is also restricted to Australia (Table 14.4). The rDNA patterns displayed by Kimberley and Arnhem Land taro represent composites of more than one kind of rDNA variant. Each pattern includes fragments

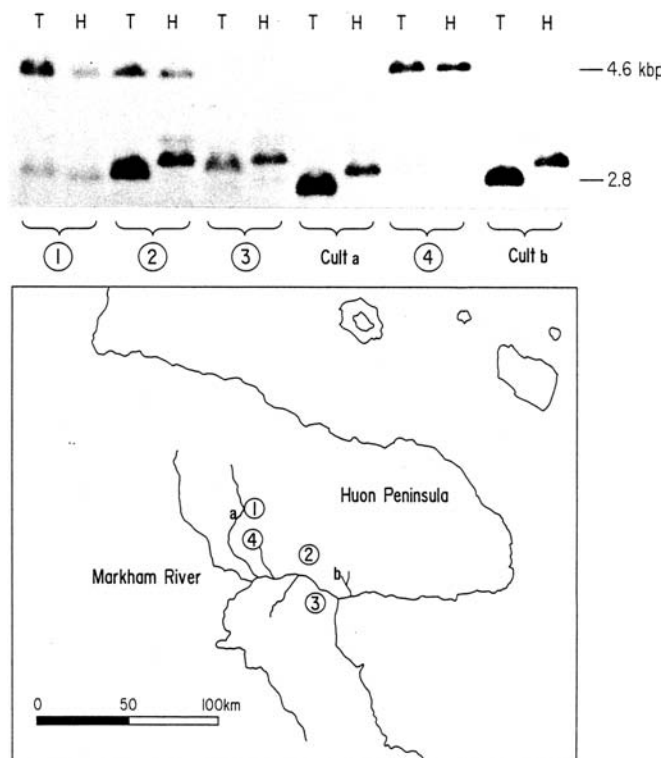


Figure 14.6 Ribosomal DNA in wild and cultivated taro, Morobe Province, Papua New Guinea. *Upper panel:* *Taq* I and *Hinf* I spacer fragments detected in an autoradiograph of one filter, after Southern transfer, and probing with the 2.8 kbp *Taq* I spacer fragment purified from pCe34.1. *Lower panel:* locations. Wild: (1) T225, Moro 2:2 pattern ($2n = 28$); (2) T226, Moro 2:3A pattern; (3) T227, Moro 2:3B pattern; (4) T229, Moro 3:3 pattern ($2n = 28$). Cultivated: (a) T228, Puk 1:2 pattern; (b) T234, Puk 1:2 pattern.

similar to those observed for Queensland, and the Queensland rDNA variant therefore appears common throughout northern Australia (Figure 14.5).

Side-by-side comparison suggests that the Queensland rDNA variant is also present in the rDNA patterns of wild and cultivated taro in Papua New Guinea (Figure 14.6). The sizes of *Taq* I and *Hinf* I spacer fragments generated by Queensland wild-type taro (2.8 kbp and 2.9 kbp) correspond closely to the modal frequency peaks for all fragments generated by these enzymes in the general survey of taro (Figure 14.1, Tables 14.1 and 14.2), and rDNA patterns were assigned to the Qld 1:1 class for samples from the eastern Pacific (Figure 14.7). The Qld 1:1 pattern is limited in distribution to the Pacific (Table 14.4), but spacer fragments similar in size to those produced by the Queensland rDNA variant are also common in Asia (Tables 14.1 and 14.2), and are possibly represented within rDNA patterns from tropical Asia (see results for widely distributed rDNA classes,

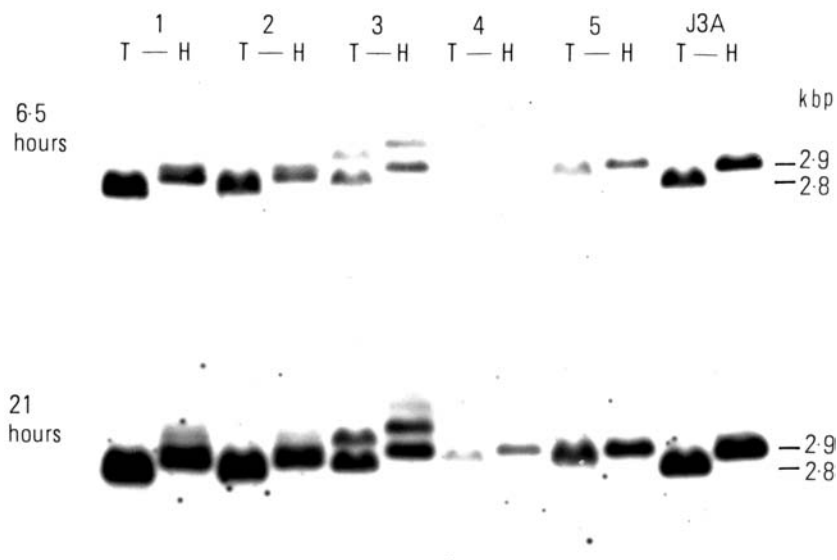


Figure 14.7 Cultivated taro from eastern Polynesia: rDNA spacer fragments detected after *Taq* I (T) and *Hinf* I (H) analysis. For each sample, the Canberra collection number, source, chromosome number, and rDNA class are as follows: (1) T117, Easter Island, $2n = 28$, East 1:3; (2) T119, Easter Island, -, East 1:3; (3) T124, Huahine Island, $2n = 28$, Puk 2:3; (4) T106, Hawai'i, -, Puk 1:2; (5) T104, Hawai'i, $2n = 28$, Qld 1:1. J3A: wild diploid from Jiyer Cave, Queensland (type sample for Qld 1:1 rDNA class).

All the Polynesian samples produced major bands like those of the Queensland rDNA variant at right (J3A), and probably possess this variant. Two exposures of the same autoradiograph are shown to illustrate the difficulty commonly encountered in assessing faint bands. T104 was assigned to the Qld 1:1 class on the basis of the 6.5 hour exposure. The result for T106 was too faint for assessment after 6.5 hours exposure, and was assigned to the Puk 1:2 class after 21 hours exposure. The faint *Hinf* I bands displayed by the Polynesian samples might represent partial digestion products rather than other rDNA variants, a possibility which cannot be resolved without replication of the tests with *Hinf* I.

below). Without replication, side-by-side analysis, and a greater range of diagnostic tests (characters) for the Queensland rDNA variant itself, it is difficult to sustain identifications of this variant far beyond Australia, because convergent length mutation in the rDNA spacer region is a real possibility (see discussion).

Wild taro in Morobe Province, Papua New Guinea, were often phenotypically similar to those in Queensland (see Figure 10.1 and 10.10, Chapter Ten). Wild plants from three locations produced very large *Taq* I and *Hinf* I fragments (c.4.6 kbp, Figure 14.6), in addition to fragments similar in size to those from Queensland. The c.4.6 kbp *Taq* I and *Hinf* I fragments were the largest observed for the species, and were found nowhere else. The DNA of T225, from site 1 in Figure 14.6, was digested with *Bam* HI, *Eco* I, *Pst* I, *Xba* I, for restriction site mapping and comparison with the restriction-site map of AKL 34 (Chapter Twelve). The results were not interpretable simply in terms of insertion or deletion within the intergenic spacer region, and as no further investigation was carried out, details are not presented here. By contrast, the restriction-site map for the Queensland rDNA variant (sample J3A), prepared with the same enzymes, was fully consistent with the map already given for AKL 34 (Chapter Twelve), with minor size differences located within the large intergenic spacer region.

Flowering was observed by the author in Morobe Province in June and July 1985, in cultivations and in the wild, and it is likely that sexual reproduction contributes to the genotypic and phenotypic heterogeneity observed for wild plants in this area.

14.3.3 Ribosomal DNA and phenotypic variation

Some rDNA classes are associated with phenotypically diverse taro, and some phenotypes are associated with diverse classes of rDNA (Table 14.5). The phenotypic categories distinguished here rely on approximate descriptions of anthocyanin distribution, so generally incorporate more than one visually distinct phenotype. The number of plants incorporated in the survey was determined, at the time of writing, by the number for which it had been possible to describe both phenotype and genotype.

Among the phenotypically homogeneous wild taro of Australia, three different rDNA classes were found (Figure 14.5, discussed above). This suggests the possibility that rDNA diversity in general is not positively correlated with phenotypic diversity. A general negative correlation is suggested by inspection of Table 14.5, as follows. In this table, approximately half the samples are in the two categories with the least extensive pigmentation (0 or 1 part pigmented, including Australian wild plants), and approximately half are in the remaining eight categories (2 to 6 parts pigmented in different combinations). Fifteen different rDNA classes are represented among 23 plants in the first two categories, and only eight different rDNA classes are represented among 21 plants in the latter eight categories. The comparison suggests that rDNA diversity in the species is negatively correlated with phenotypic diversity. An explanation is proposed later.

Table 14.5 Classification of 44 samples of *C. esculenta* according to rDNA class and the distribution of anthocyanin pigments. No phenotype descriptions were available for the Moro 2:2, Ruti 3:2B rDNA classes reported in Table 14.3. The presence (+) or absence (-) of anthocyanins is shown for seven parts of the plant: (1) leaf, including blade and petiole; (2) basal ring; (3) roots; (4) corm skin; (5) corm cortex parenchyma; (6) corm core parenchyma; (7) corm core fibres. Ribosomal DNA classes are described in Table 14.3 and the phenotypic characters are described in Chapter 10.

PhenotypicClass								Ribosomal DNA Class																	
Anthocyanin distribution								Old	Puk	East	Buk	Am	Kim	Bay	Col	Moro	Moro	Puk	Kat	Min	Ruti	Moro	Col	Eli	Kat
1	2	3	4	5	6	7		1:1	1:2	1:3	2:1	2:2	2:2	2:2	2:2	2:3A	2:3B	2:3	2:3	3:2	3:2A	3:3	3:4	3:5	4:4
-	-	-	-	-	-	-		2	1			1	2			1		2				1			
+	-	-	-	-	-	-			3					1	1		1	2	1	1			1	1	1
+	+	-	-	-	-	-																	2		
-	+	+	-	-	-	-												1							
+	+	+	-	-	-	-																	1		
-	+	+	+	-	-	-		1																	
+	+	+	+	-	-	-		1	6	2				1				2			1				
+	-	+	+	-	-	+													1						
+	+	+	+	-	-	+													1						
+	+	+	+	+	+	-					1														

14.3.4 Ribosomal DNA and chromosome numbers

Diploid and triploid taro display wide spacer-fragment size ranges (Table 14.6), relative to the ranges observed overall (Tables 14.1 and 14.2). Diversity is also apparent in the range of rDNA classes found among diploid and triploid taro (Table 14.7). Three known triploids gave rDNA patterns (Eli 3:5, and Kat 4:4) more complex than any shown by the known diploids. This is consistent with the greater potential for heterozygosity in triploids (three potentially different sets of chromosomes rather than just two), but complex rDNA patterns do not necessarily reflect chromosomal heterozygosity (see discussion).

14.3.5 New Zealand and Japanese Triploids

Triploid cultivars from Japan were tested with *Taq* I and *Rsa* I (Figure 14.8). In combination, these two enzymes define three classes of rDNA pattern (A to C), which show congruence with Japanese botanical group identifications (Table 14.8). The New Zealand triploid varieties RR and GR (generally cultivated) and GP (generally wild) were previously tested with *Taq* I, *Rsa* I partial digestion, and *Bam* HI (Chapter Eleven, Figures 11.9 to 11.11). In these tests, varieties RR and GR were indistinguishable from each other, and were distinct from var. GP. The grouping of varieties RR and GR and their separation from var. GP is also apparent after complete *Rsa* I digestion. Three *Rsa* I bands produced by var. RR and var. GR are clearly a sub-set of the *Rsa* I bands shown by Japanese varieties of the triploid *Eguimo* group (Figure 14.9). The variety GP may

Table 14.6 Size frequency distributions for *Taq* I and *Hinf* I rDNA spacer fragments in diploids ($2n = 28$) and triploids ($2n = 42$). Although both diploid and triploid taro display a wide range of rDNA fragment sizes, most of the spacer fragments in each ploidy level are within or close to the modal size classes recorded for the species generally (see Figure 14.1, size classes 2.7–2.89 kbp for *Taq* I, 2.9–3.29 kbp for *Hinf* I). The number of assays (plants used) for each ploidy level is shown below. Appendix 20 lists the accessions for which both rDNA analyses and chromosome counts were made.

Size class kbp	Taq I		Hinf I	
	2n = 28	2n = 42	2n = 28	2n = 42
1.9 – 2.09	1	1		
2.1 – 2.29		1		
2.3 – 2.49			1	
2.5 – 2.69		1		
2.7 – 2.89	10	8	5	1
2.9 – 3.09	5	3	8	1
3.1 – 3.29	3	12	8	3
3.3 – 3.49	4	4	2	4
3.5 – 3.69	1	2	1	2
3.7 – 3.89		1	1	2
3.9 – 4.09		1		
4.1 – 4.29				1
4.3 – 4.49				
4.5 – 4.69	1		1	
Total Assays	16	17	13	6

Table 14.7 Ribosomal DNA classes in diploids ($2n = 28$) and triploids ($2n = 42$). The classes are listed in order of increasing complexity, that is, the number of different *Taq* I and *Hinf* I spacer fragments, as indicated by the ratios. Data from 11 accessions of taro.

rDNA class	2n = 28	2n = 42
Old 1:1	2	
East 1:3	1	
Kim 2:2	1	
Puk 2:3	2	
Kat 2:3		1
Moro 3:3	1	
Eli 3:4		2
Kat 4:4		1

also be related to *Eguimo*, but the apparent affinity is weaker because it depends on a comparison of only two rDNA bands (Figure 14.9, *Taq* 2.8 kbp probe).

The 1.6 kbp *Rsa* I fragment shared by samples 1 to 5 may be a conserved DNA sequence from a genic region flanking the intergenic spacer, and may also be produced

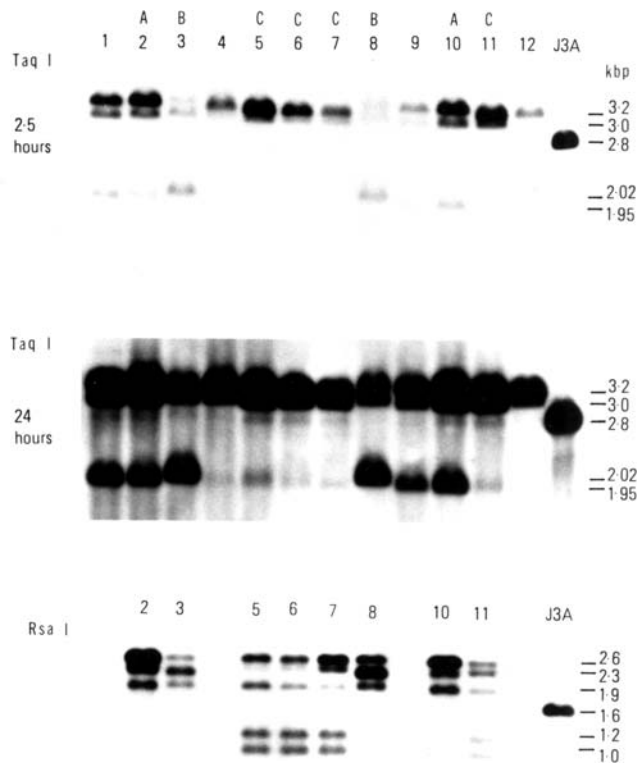


Figure 14.8 Japanese taro (samples 1–12), mostly cultivated: rDNA spacer fragments detected in autoradiographs after Southern transfer. The *Taq* I fragments were probed with pCe34.1; *Rsa* I fragments were probed with the 2.8 kbp *Taq* I spacer fragment excised from pCe34.1. Ribosomal DNA classes A–C, recognised here according to the combined results of *Taq* I and *Rsa* I analysis, are indicated at top. For each sample, the Canberra collection number, source, habitat, varietal group name, and chromosome number (if recorded) are as follows: (1) T293, Tokushima, cultivated, var. *Kuraimo*, $2n = 42$; (2) T294, Takushima, cultivated, var. *Syogaimo*, $2n = 42$; (3) T296, Kōchi, cultivated, var. *Erikake*; (4) T297, Kōchi, cultivated, var. *Eguimo*; (5) T298, Kōchi, cultivated, var. *Eguimo*; (6) T29-9, Kōchi, cultivated, var. *Eguimo*, $2n = 42$; (7) T302, Nagano, wild, var. *Kōbōimo*, $2n = 42$; (8) T303, Ehime, cultivated, var. *Erikake*; (9) T305, Kōchi, cultivated, var. *Kuraimo*; (10) T306, Kōchi, cultivated, var. *Eguimo*; (11) T326, Osaka, cultivated, vernacular var. *Ishikawawase*. J3A: wild diploid from Jiye Cave, Queensland (type sample for Qld 1:1 rDNA class).

After 24 hours exposure, the Japanese taro display a faint *Taq* I band similar in size to the 2.8 kbp band that characterises the Queensland rDNA variant at right. This suggests that the Queensland rDNA variant is present in the triploid varieties in low copy number. More detailed analysis is required to confirm this.

Table 14.8 Summary of DNA and phenotype observations for eight accessions of Japanese taro, all from cultivations except T302, which was from the wild. Ribosomal DNA classes, A–C, are defined according to *Taq* I and *Rsa* I intergenic spacer fragments (see Figure 14.8). The phenotypic characters are described in Chapter Ten.

Group name = botanical name applied by the Japanese collectors. Vernacular name = name used by the growers. The chromosome numbers were provided by T. Kawahara, except for T294, which was examined by P. Gaffey. Asterisks indicate accessions, which belong to botanical varieties which are typically triploid (Kawahara pers. comm. 1985). Accession numbers are given for the Kyoto Plant Germplasm Institute (KPGI), and the Australian National University (ANU).

rDNA class	A	A	B	B	C	C	C	C	
Group name	Shōgaimo	Kuraimo	Erikake	Erikake	Eguimo	Eguimo	Eguimo ¹⁾	Eguimo	
Vernacular name	Yatsume	Kuraimo	Bon'imo	Erikake	Eguimo, Shimaimo	Shimaimo	Kōbōimo	?	
Chromosome no.		42*	*	*	?	42	42	?	
Blade vascular	?	green	green	green	green	green	green	green	
Blade laminar	?	green	green	green	green	green	green	green	
Petiole graded	?	green	green/ purple	purple/ green	green/ purple	green/ purple	green/ purple	green/ purple	
Petiole variegated	?	no	no	no	no	no	no	yes	
Basal ring	?	white	white	white	white	white	white	white	
Roots	?	white	white	white	white	white	white	white	
Skin	?	white	white	white	white	white	white	white	
Cortex	?	white	white	white	white	white	white	white	
Core	?	white	white	white	white	white	white	white	
Fibres	?	white	white	white	white	pale yellow	yellow	white	
side-shoots	?	cormels	cormels	cormels	cormels	cormels	cormels	cormels	
Locality	Tanima	Ōkage	Uriuno	Iwagaichi	Nakamine	Iwagara	Kutsukake- onsen	Kubo- Wakubo	
Prefecture	Toku- shima	Kōchi	Kōchi	Ehime	Kōchi	Kōchi	Nagano	Kōchi	
KPGI no.		7210	7308	7221	7304	7237	7245	7301	7309
ANUT no.		294	305	296	303	298	299	302	306

by J3A. The result for J3A is obscured by the presence of 1.6 kbp spacer fragments, as demonstrated by analysis with the *Taq* 2.8 kbp probe, below. All the other fragments are clearly diagnostic, and each of the New Zealand varieties display spacer fragments similar to those produced by the Japanese triploid variety *Eguimo*.

Very long exposure of the *Taq* I fragments from Japanese taro reveals a very faint 2.8 kbp band, suggesting that the Queensland rDNA variant is present in very low copy number (Figure 14.8).

This result, and the preceding comparisons, are discussed later with regard to the origins of the Queensland rDNA variant and the origins of New Zealand and Japanese triploid taro.

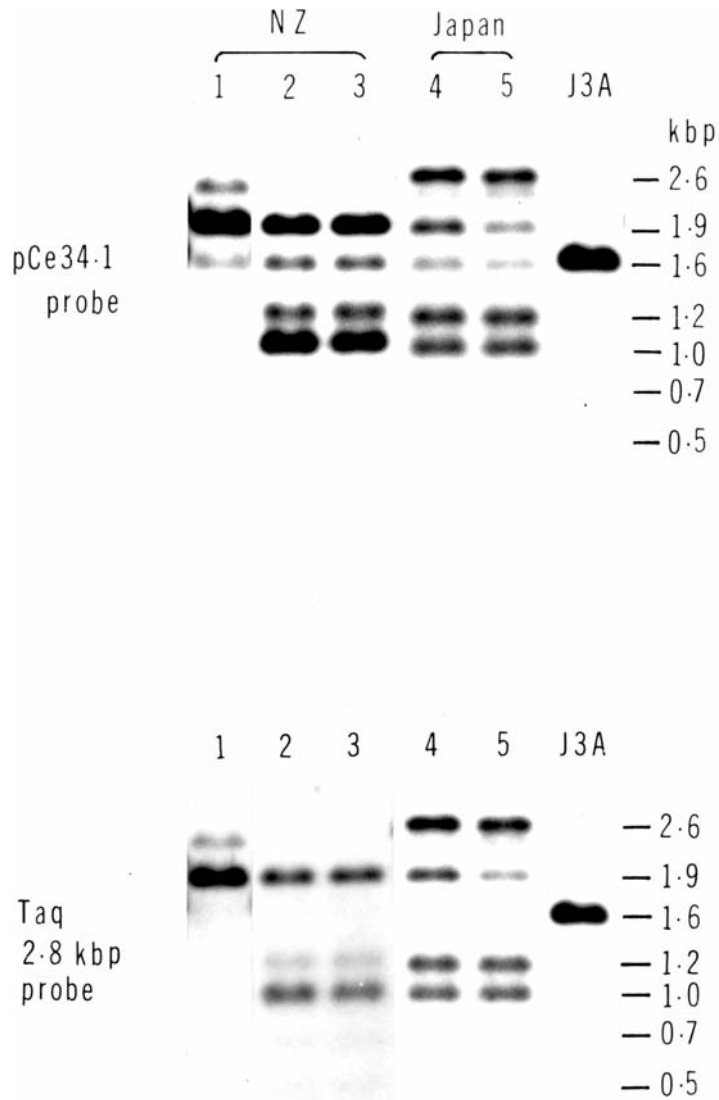


Figure 14.9 Comparison of triploid taro varieties from New Zealand and Japan. Autoradiographs of *Rsa* I fragments after probing with pCe34.1 (above) and the 2.8 kbp *Taq* I spacer fragment excised from pCe34.1 (below). For each sample, the Canberra collection number, source, habitat, variety name, and chromosome number (if recorded) are as follows: (1) T285, Bay of Islands, wild, var. GP, $2n = 42$; (2) T272, Bay of Islands, wild, var. RR, $2n = 42$; (3) T279, East Cape, from a garden, var. GR, $2n = 42$; (4) T298, Kōchi, cultivated, var. *Eguimo*; (5) T299, Kōchi, cultivated, var. *Eguimo*, $2n = 42$. J3A: wild diploid from Jiyer Cave, Queensland.

14.3.6 Widely distributed rDNA classes

Three rDNA classes, well defined by multiple bands of *Taq* I and *Hinf* I fragments, were found over very wide ranges. The type accessions and locations are T323, wild, from Colombo, Sri Lanka (Col 3:4 class), T188, cultivated at Pukanti, Papua New Guinea (Puk 2:3 class), and T322, wild near Eliya, Sri Lanka (Eli 3:5 class). The Col 3:4 class (Figure 14.10) was observed for accessions from Madagascar (cultivated), Sri Lanka (wild but probably feral, in urban area) and Japan (cultivated). The Puk 2:3 class (Figure 14.10) was observed for accessions from Madagascar (cultivated), the Philippines (cultivated), Papua New Guinea (cultivated and wild), Tonga (cultivated), and Huahine in the Society Islands, eastern Polynesia (cultivated). Analyses with *Rsa* I confirmed the similarity between accessions from Madagascar and Papua New Guinea (Figure 14.11), and the Philippines (results not presented because of poor autoradiographs).

The Eli 3:5 class (Figure 14.11) was observed for all accessions of *C. esculenta* var. *fontanesii* Schott, from Sri Lanka (wild), Australia (cultivated ornamental) and New Zealand (cultivated ornamental).

For each sample, the Canberra collection number, source, habitat, and chromosome number (if recorded) are as follows: Puk 2:3 class: (1) T1, Kuk, Western Highlands, cultivated, $2n = 28$; (2) T167, Ruti, Western Highlands, wild; (3) T188, Pukanti, Western Highlands, cultivated; (4) T190, Pukanti, Western Highlands, cultivated; (5) T193,

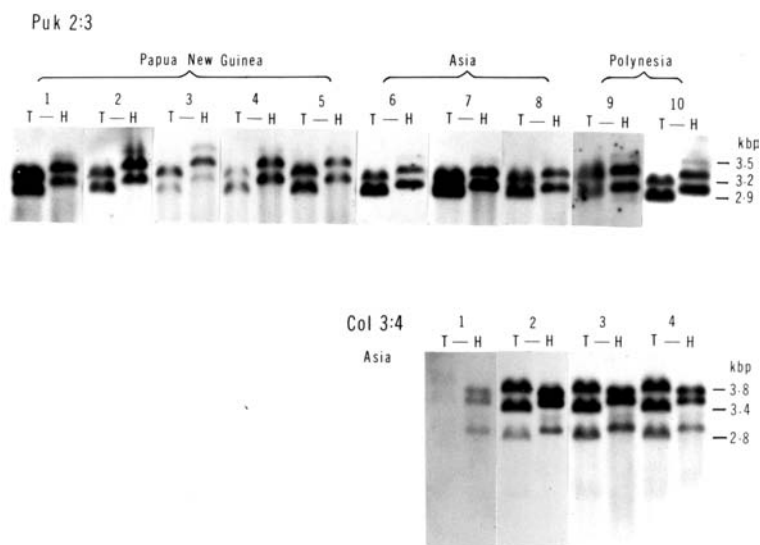


Figure 14.10 Widely distributed rDNA classes: Puk 2:3 and Col 3:4. *Taq* I (T) and *Hinf* I (H) spacer fragments detected in autoradiographs after Southern transfer and probing with pCe34.1 or the 2.8 kbp *Taq* I spacer fragment excised from pCe34.1. Results compiled from several separate autoradiographs, and size estimates based on the average for each rDNA class (Table 14.3). The uppermost *Hinf* I band is often faint and indistinct, and is possibly a product of partial digestion.

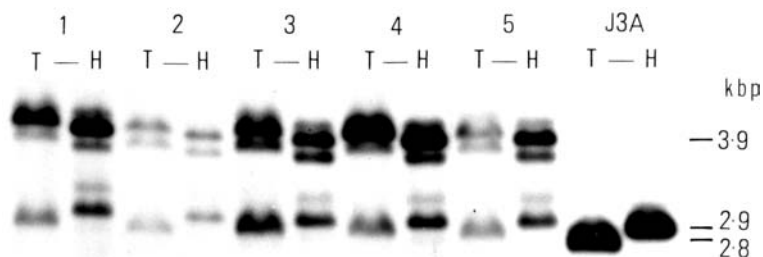


Figure 14.11 *C. esculenta* var. *fontanesii*: intergenic spacer fragments (samples 1–5). *Taq* I (T) and *Hinf* I (H) fragments detected with pCe34.1 after Southern transfer. No variation is observed between accessions. The combined pattern of *Taq* I and *Hinf* I fragments from this variety has been named Eli 3:5.

Samples: (1) T264, ornamental, Urunga, Australia, $2n = 42$; (2) T291, ornamental, Kaitaia, New Zealand; (3) T330, ornamental, Sydney, Australia; (4) T339, ornamental, Melbourne, Australia; (5) wild, between Nuwara and Eliya, Sri Lanka, $2n = 42$. J3A: wild diploid from Jiyer Cave, Queensland.

Pukanti, Western Highlands, cultivated; (6) T131, Luzon, Philippines, cultivated; (7) T363, Madagascar, cultivated; (8) T366, Madagascar, cultivated; (9) field collection only, Tonga, cultivated; (10) T124, Huahine Island, cultivated, $2n = 28$.

Col 3:4 class: (1) T327, Kyoto markets, vern. *Akame-ebi-imo* possibly from Shikoku, southern Japan, cultivated (faint *Taq* I bands visible in original autoradiograph); (2) T323, Colombo, Sri Lanka, wild; (3) T364, Madagascar, cultivated; (4) T365, Madagascar, cultivated.

This variety, described by Engler and Krause (1920), is commonly cultivated as an ornamental in Australia and New Zealand (observation by P. J. Matthews). Cultivated plants collected in Australia and New Zealand were phenotypically identical to the wild plant collected from Sri Lanka (see Figure 10.2, Chapter Ten), and chromosome counts of $2n = 42$ (triploid) were made for T322, from Sri Lanka, and T264 from Urunga, Australia.

Each of the widely distributed classes described above is in part characterised by spacer fragments similar in size to those produced by the Queensland rDNA variant, an observation of interest for discussing the possible origins of this variant, below.

14.4 Discussion

14.4.1 The Queensland rDNA variant

The survey of wild taro in Queensland established the existence of a single rDNA size variant in this area, characterised in part by analysis of *Taq* I and *Hinf* I fragments. The Queensland rDNA variant may be geographically widespread because *Taq* I and *Hinf* I spacer fragments, similar in size to those from Queensland, were observed for many taro from beyond Queensland, in other parts of Australia, and in Asia, and the Pacific. However, the possibility of convergent mutation makes it difficult to identify with

certainly the Queensland rDNA variant in plants from beyond Queensland.

It is a well-established general observation for diverse plant and animal taxa, and within species, that intergenic spacers vary in length because of deletions and insertions of short sequence motifs (sub-repeats) within the spacers (Appels and Honeycutt 1986; see also Chapter Nine). Such mutations can independently generate rDNA variants of similar length in diverse taxa, and in different genetic lineages within species. During the long-term evolutionary history of *C. esculenta*, rDNA variants of similar length to the Queensland variant may have become common because of convergent mutation and an as yet unknown selective advantage or molecular mechanism allowing them to proliferate within individuals, clonal lineages, and sexually reproducing populations.

The alternative to convergence, as a general explanation, is that the Queensland rDNA variant is monophyletic. The two major alternatives, polyphyletic versus monophyletic origin, cannot be resolved without closer characterisation of the Queensland rDNA variant itself. More diagnostic restriction enzyme tests for spacer and genic regions are needed so that rDNA variants are not distinguished solely in terms of intergenic spacer length. If convergent mutation did occur, its actual historical significance might not be great. Intensive studies of rDNA evolution in wheat (*Triticum* spp) have been carried out over recent years, and provide precedents for both hypotheses. It is sufficient here to note the precedents, without critical examination, as follows.

In Figure 14.12, the unimodal size frequency distribution for Taq I fragments from taro can be compared to the similar size frequency distribution (Flavell et al. 1986) for *Triticum dicoccoides*, a wild tetraploid wheat in Israel and neighbouring areas. Similar numbers of plants were examined, but the geographical range of *T. dicoccoides* is much smaller than that of taro. The DNA analyses for taro were conducted on the clonal offspring of vegetative shoots collected in the field, or directly on leaf samples from the field, while analyses for *T. dicoccoides* were conducted on individual seedlings taken from individual self-fertilised lines, established an unspecified number of generations previously with seed collected in the field. Flavell et al. (1986) are confident that the unimodal peak is indicative of the actual size frequency distribution for the species. The size frequency distribution for taro may also be representative for the species despite the likely inclusion of partial digestion products (as noted for the Puk 1:2 class, for example), and despite geographical sampling biases. The Taq I fragment that was most widespread among wheat populations was found in the least variable populations, and was in the most abundant size class (2.9–3.1 kbp, Figure 14.12). This variant was interpreted as representing a generally optimum spacer length maintained in high frequency by selection. Variance in the number of different spacer length variants, within populations, was found to be correlated with an index of climate, and it was suggested that spacer length polymorphisms represent regulatory adaptations to environmental factors, following indications elsewhere that the intergenic spacer regions are involved in regulating rRNA gene expression. Flavell et al. (1986) do not regard the present range of rDNA size variation as being related to founding effects, and therefore imply that rDNA size variation today is largely the product of frequent mutation coupled with differential selection. This sets a precedent for suggesting the polyphyletic origins of rDNA size

variants like the Queensland variant, and for the maintenance of such variants as a predominant class in the species by selection.

In another study of *Triticum* by Vinitsky et al. (1989), the nucleotide sequence of a large intergenic spacer from the *Nor-D3a* allele of *T. tauschii* (DD genomes) was compared to the sequence of a spacer from the same allele (rDNA variant) present in the hexaploid bread wheat, *Triticum aestivum* (AABBDD genomes). The species *T. tauschii* is regarded as one of the progenitors of *T. aestivum*. The two spacers compared were virtually identical in sequence, with an unchanged number of sub-repeats. In the period since the progenitor species contributed its *Nor-D3a* spacer length variant, at formation of the hexaploid, the intergenic spacers of the progenitor species and its descendant have not changed. These two species are believed to have been reproductively isolated from each other for at least 6,000 to 8,000 years (Vinitsky et al. 1989), so the *Nor-D3a* rDNA variant has been stably transmitted across sexual generations for at least this length of time. This example shows that the Queensland rDNA variant could be monophyletic and

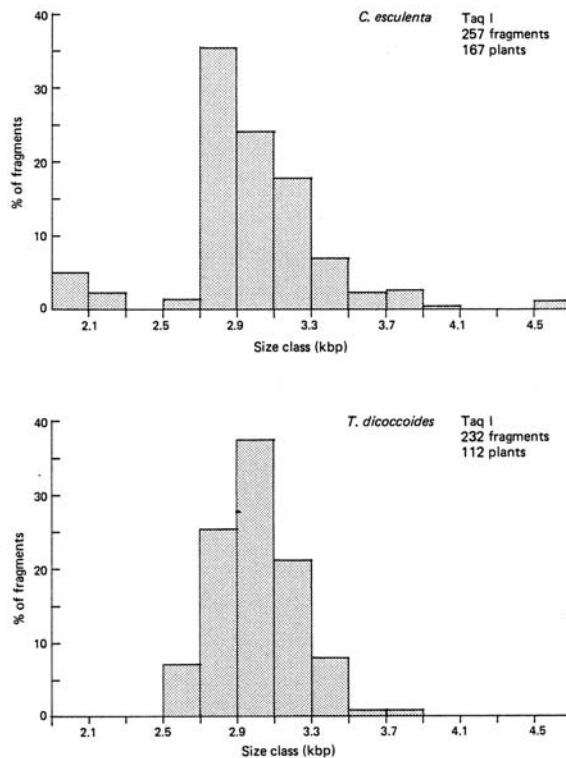


Figure 14.12 Percentage frequencies of rDNA intergenic spacer fragments in different size classes: *Taq* I fragments from *C. esculenta* (taro) and *Triticum dicoccoides* (a wild tetraploid wheat). For taro, 257 fragments were detected in 167 plants (data from Table 14.1); for wheat, 232 fragments were detected in 112 plants (data from Flavell et al. 1986).

ancient, and could have existed for thousands of years during the dispersal of taro through Asia and the Pacific by natural means or otherwise.

Ribosomal DNA variants represented in the patterns produced by Japanese triploid taro (Figure 14.8) and the triploid var. *fontanesii* from Sri Lanka (Figure 14.11) might prove on closer inspection to be identical to the Queensland rDNA variant. Assuming monophyly, such a result would suggest that the Queensland rDNA variant existed in diploid progenitors shared by the Japanese and Sri Lankan triploids. The reduced copy number of the Queensland rDNA variant (not definitely identified) in the triploids from temperate Japan, and the apparent prominence of this variant in plants from tropical parts of Asia and the Pacific, suggest that taro in temperate and tropical areas may have diverged genetically. Closer characterisation of rDNA and more extensive geographical surveys beyond Queensland are needed to determine the ultimate genetic and geographical origins of the Queensland rDNA variant.

14.4.2 Taro in Australia

In order to clarify the status of wild taro populations in Queensland, some observations regarding cultivated taro are necessary.

Information on cultivated taro in Australia is either anecdotal or from personal observation in Queensland. Often it is stated that Melanesian sugar-cane workers were responsible for the introduction of taro to Queensland during the last 150 years (for example, Fatanowna 1989: 110) but there are other possible sources. These include Chinese growers and traders, first associated with gold mining last century (Choi 1975), missionaries, recent twentieth-century immigrants from Asia and the Pacific, plant collectors (working for botanical gardens, for example), and importers of ornamental plants.

In Queensland, cultivated plants were found on three properties, near Cairns, Ingham, and Mackay. These plants were phenotypically similar to each other and to taro found growing wild on two farms near Ingham and Mackay. The wild patch near Ingham is occasionally harvested by a local Aboriginal and Torres Strait Islander family (T. Palmis, Ingham, pers. comm. 1987). A small clump of wild taro, also similar phenotypically to those found cultivated, was found very near the remains of a major gold-mining camp on the lower Russell River. It is quite possible that the variety here was previously cultivated at the camp. R. Tucker (Townsville pers. comm. 1987) reports the existence of about thirty taro cultivars in North Queensland, none of which persist in the wild, in his experience.

Cultivated taro has been a very minor crop in Queensland, and despite introductions over the last 150 years there has been little dispersal of cultivated varieties into the wild. All the Queensland varieties cultivated for food and seen by the author were phenotypically distinct from the single wild phenotype that is common in Queensland. One plant, found wild on a farm near Mackay, was phenotypically similar to Queensland cultivated taro and yielded a *Taq* I pattern (result not presented) unlike the common pattern found in Queensland wild taro, and unlike the patterns of wild taro in Arnhem Land and Kimberley.

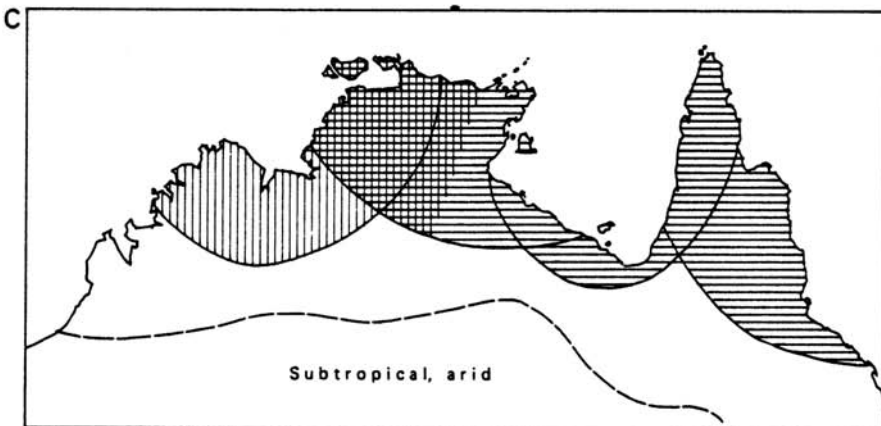
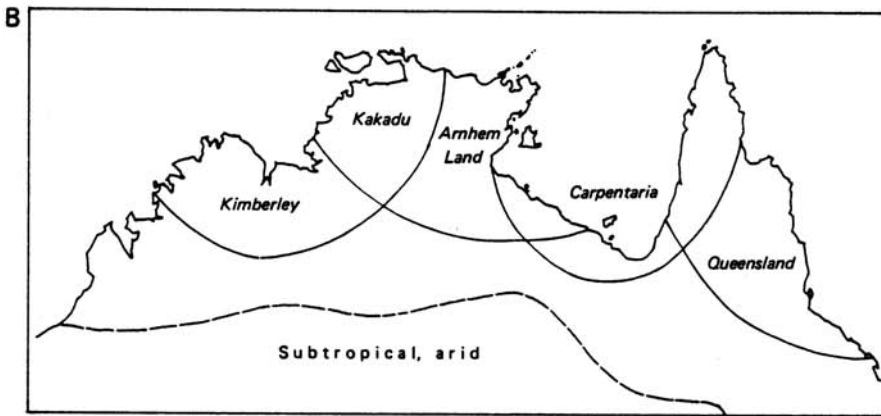
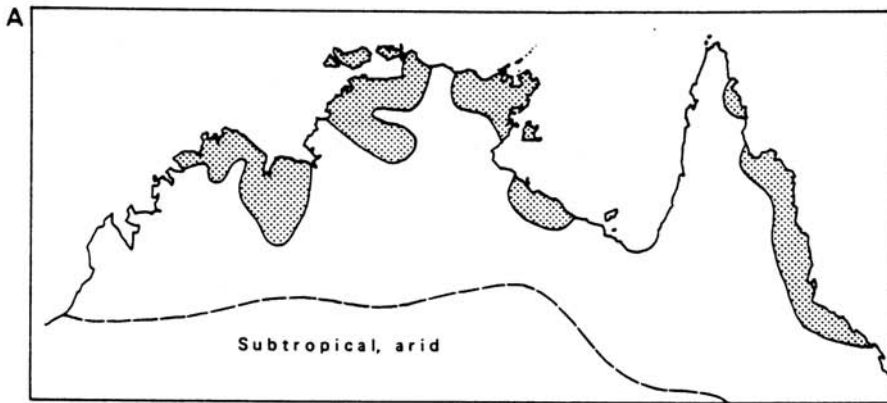
In Queensland, some wild patches in areas of rural settlement undoubtedly have a history of initial planting, occasional harvest, and replanting for maintenance, similar to the history of wild patches seen recently (Matthews 1985) in rural northern New Zealand.

There is however no evidence for a general movement of recently introduced varieties into the wild in Australia. The following discussion refers to wild taro derived from wild populations that existed before European settlement. The early botanical records (Chapters 9 and 10) leave no doubt that such populations existed.

Neither natural dispersal nor humans appear to have caused wide-scale mixing of rDNA variants in wild taro across northern Australia (Figure 14.5). Natural animal vectors for fruit and seed have not been seen, but could be ground-feeding species of birds, rodents, or small marsupials, since the fruiting heads of taro droop towards the ground and eventually drop when mature (personal observation). Natural vegetative dispersal is limited to downstream displacement by water. Pollinating insects (also not yet identified) and fruit-eating animals could, in theory, facilitate gene flow across country between water systems. Limits to dispersal by humans may have been determined by environmental barriers to human movement, frequency of utilisation, transplantation practices, and/or social boundaries. Whatever the limits were, for the dispersal of taro, they must have changed over time according to changing natural and social circumstances. The existence today of different forms of wild taro in different areas, as detected by rDNA analysis, provides a starting point for biological approaches to determining the origins, antiquity, and dispersal of taro in Australia. The discussion below focuses on the analysis of genotypic variation within taro. In Chapter Fifteen, attention is given to other kinds of biological evidence relevant to the origins and dispersal of taro in Australia and New Guinea.

Figure 14.13 presents some purely hypothetical models for the distribution of genotypic variation in wild taro in Australia, based on the known distribution range of taro and on the known distribution of rDNA variation within that range. Future analysis of other aspects of genotype may detect variation that coincides in its geographical distribution with distribution of rDNA variation (Figure 14.13, A). This would confirm the absence of dispersal between areas. Alternatively, there may have been mixing of the known rDNA variants between geographical areas, with no intra-individual genotypic mixing (Figure 14.13, B). This would imply that no natural sexual breeding and dispersal occurred, and that vegetative dispersal by humans was prevalent and led to mixing between water systems.

If the distribution of other kinds of genotypic variation does not coincide with the distribution of rDNA variation (Figure 14.13, C), then some kind of natural gene flow would be indicated. Human dispersal of vegetative parts involves entire, non-segregating nuclear genomes, together with chloroplasts and mitochondria, whereas natural dispersal of seed and pollen provides opportunities for the differential movement of chloroplasts, mitochondria, and nuclear chromosomes. Nuclear chromosomes probably disperse more freely than chloroplasts and mitochondria, because these latter are not carried by pollen, if taro is like most other plants. If natural and differential gene flow is detected, then its nature and extent would have implications for the antiquity of taro in Australia (and New



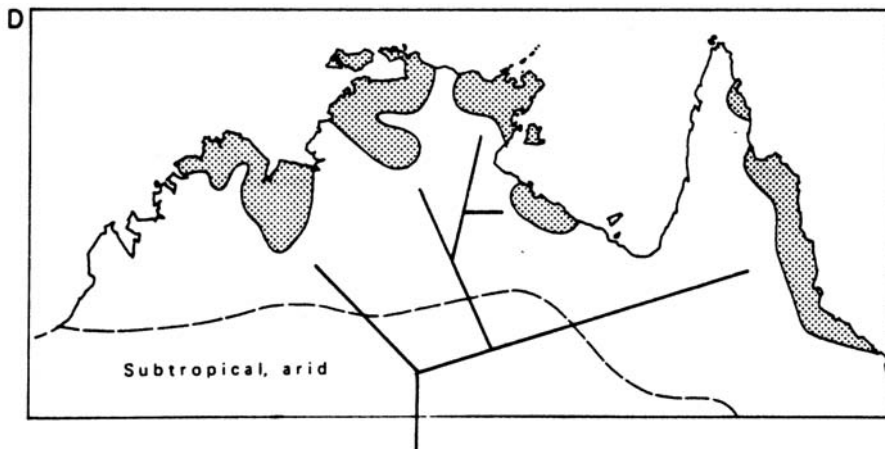


Figure 14.13 Wild taro in Australia: Hypothetical models relating possible dispersal processes in the past to outcomes that might, in theory, be observed in the present by combining field surveys and genotypic analysis.

- A. No dispersal, natural or otherwise, occurred between the different areas known to possess wild taro (shaded areas, from Chapter Ten, Figure 10.11), or between the regions defined by the distribution of rDNA variation (see Figure 14.5). The spatial patterns of genotypic variation arising within each region are entirely derived from local reproduction and dispersal, subsequent to separate colonisations by taro.
- B. The present range of taro resulted from the dispersal of vegetative parts by humans and natural dispersal via sexual reproduction did not occur. The distributions of rDNA variants (indicated here by curves) overlap, but intra-individual mixtures of rDNA classes are absent, proving that sexual reproduction did not occur (i.e., all heterozygosity is fixed).
- C. Natural long-distance dispersal occurred (this would necessarily involve sexual reproduction). The overlapping distributions of rDNA classes are indicated by curves, and the distributions of other kinds of genotypic variation are represented by horizontal and vertical lines. The different kinds of genotypic variation do not coincide in their geographical distributions, and a lack of fixed heterozygosity proves that sexual reproduction occurred. The genetic effects of humans transporting and planting vegetative parts are obscured by natural breeding and dispersal.
- D. Endemic differentiation occurred and the phylogenetic relationships of the different varieties that resulted are correlated with their geographical distributions (shaded areas). The species was present long enough for mutation, and dispersal by natural or other means was not sufficient to prevent regional differentiation.

Guinea also, due to its proximity within the continent of Sahul).

Future studies of rDNA and other aspects of genotype, and wider surveys outside Australia, might show that the rDNA variants observed here are endemic to Australia, together with other genotypic traits. The degree of endemic differentiation would, in itself, be some measure of antiquity, and a large degree of differentiation would be strong evidence that taro colonised Australia by natural means, before humans. If the endemic traits also allow phylogenetic interpretation (Figure 14.13, D), then relating geography and phylogeny would strengthen interpretations of endemism, antiquity, origins, and dispersal.

There already exist two potential tests for detecting sexual reproduction and natural gene flow in Australian wild taro. The Kim 2:2 and Arn 2:2 classes may each represent a simple heterozygous condition, i.e., each may possess a single rDNA locus, associated with one homologous pair of chromosomes and two alleles. If, for example, this is the case in Arnhem Land, and sexual reproduction occurs, then it should be possible to find two homozygous patterns, one composed of small *Taq* I and *Hinf* I fragments, and one composed of fragments like those found in Queensland (Qld 1:1 class). If only fixed heterozygosity is found, this would suggest the purely vegetative dispersal of a heterozygous clone.

The other potential test is cytological. Coates et al. (1988) recorded the presence of a single acrocentric chromosome among the metacentrics of a diploid wild taro from Australia (cytotype I-1). This heterozygous cytotype was recorded in Queensland (Yen pers. comm. 1988). If sexual reproduction was important for the dispersal of taro within Queensland, then it should be possible to find cytotypes that are homozygous acrocentric, homozygous metacentric, and heterozygous acrocentric, and heterozygous metacentric.

If dispersal in Queensland began in the north and then proceeded southwards, then this might be evident in a decline of heterozygosity in local populations from north to south. Alternatively, if fixed (100%) heterozygosity is found in all populations, this would be a strong indication that all reproduction was vegetative (and all seed non-viable), and that human dispersal was therefore entirely responsible for the movement of wild taro between water systems within Queensland.²⁾

14.4.3 Taro in Papua New Guinea and Oceanic Pacific Islands

Two main points of interest arise from the survey of taro in Papua New Guinea. First, the wild taro of Morobe Province are phenotypically similar to wild taro in Australia, but display an rDNA pattern that is distinct from the three Australian rDNA patterns and distinct from all cultivated taro tested for Asia and the Pacific. There may have been natural and endemic differentiation of wild taro in Papua New Guinea, as was proposed for Australia above. Secondly, assuming that the Queensland rDNA variant is monophyletic and ancient, then comparisons of *Taq* I and *Hinf* I spacer fragments suggest that this variant occurs in cultivated and wild taro in Papua New Guinea. If the Queensland variant proves to have originated in Sahul, then it will provide a marker for the indigenous cultivation and domestication of natural and/or new wild varieties originating in New Guinea.

If the Queensland rDNA variant is monophyletic and ancient within the species, with an origin in mainland Asia, then its occurrence in Pacific island cultivars would not necessarily have resulted from indigenous selection and domestication in New Guinea. The comparisons of *Taq* I and *Hinf* I fragments suggest that the Queensland rDNA variant is present in Pacific island cultivars, but the significance of this for the origins of oceanic island taro will not be known until the ultimate origin of the Queensland rDNA variant is known.

Two key areas for investigating the origins of wild taro and the Queensland rDNA variant in Sahul are the southern coast of Papua New Guinea and the islands of

Indonesia, west of Wallace's line. It is predicted that wild taro in the Fly River district, close to Northeast Queensland, will be found to possess the Queensland rDNA variant. If the Fly River taro are identical or most closely related to Queensland wild taro, this would confirm the shared recent evolutionary history of taro in Australia and New Guinea. Indonesia is probably the most recent ancestral area for wild taro in Sahul. If the wild taro of Indonesia are different, this would be good evidence for endemism in Sahul, unless the immediate origins of taro in Sahul lie beyond Indonesia. If wild taro in Sahul are more closely related to wild taro elsewhere than Indonesia, in Asia, then long-distance dispersal by humans might explain the apparent biogeographical disjunction.

14.4.4 Ribosomal DNA and phenotypic variation

Clawson (1985) suggested that positive selection for colour variation has been a general phenomenon for cultivated plant species, and this might also be true for *C. esculenta*. Anthocyanin pigments were not totally absent from wild taro in Australia and New Guinea. Red or purple colouring at the junction of the petiole and the blade was sometimes evident in the wild, not always on all the leaves of one plant displaying these pigments. Among taro collections generally, red or purple pigments were noted in responses by true roots (not the corms) to wounding or cramping when potted. The petioles of *C. fallax* were purple (Figure 10.4) and the blades of *C. affinis* displayed purple patches (Figure 10.5). Whether or not these are natural phenotypes for *C. fallax* and *C. affinis* remains to be verified in the field, as the available examples were unprovenanced horticultural curios. With these examples of pigmentation in the possibly natural wild taro varieties, and in species closely related to taro, the ability to produce anthocyanins cannot be completely excluded as a primitive trait for taro.

In Figure 14.14 a simplified historical scheme is proposed, based on the apparent inverse relationship between rDNA variability and phenotypic variability (see Table 14.5, results) and two assumptions. The assumptions are that less pigmented phenotypes represent a primitive condition within the species, and that most rDNA diversity evolved over a long period of time before selection and propagation by humans. A possible explanation is that selection by humans promoted variability in the expression of already existing anthocyanin genes, leading to the diverse colour patterns as observed in cultivars today. Whatever the details of the actual process, the evident outcome for cultivated taro is that more extensively and variably coloured varieties, as a group, exhibit less rDNA variation than less extensively pigmented varieties.

The same inverse relationship might apply to genes of agronomic significance. Colour variation is commonly used in the field to recognise different varieties, but as a guide for field sampling, it may fail to maximise sampled variation for genes affecting agronomic characters. In other words, there may be no general rule for relating colour variability and the variability of genes for other agronomic characters. The inverse relationship with colour variation may apply more generally to genes which have not been of agronomic importance.

Ribosomal DNA spacer variability in taro may or may not have been of agronomic importance in the past. This question is beyond the scope of the present thesis. However,

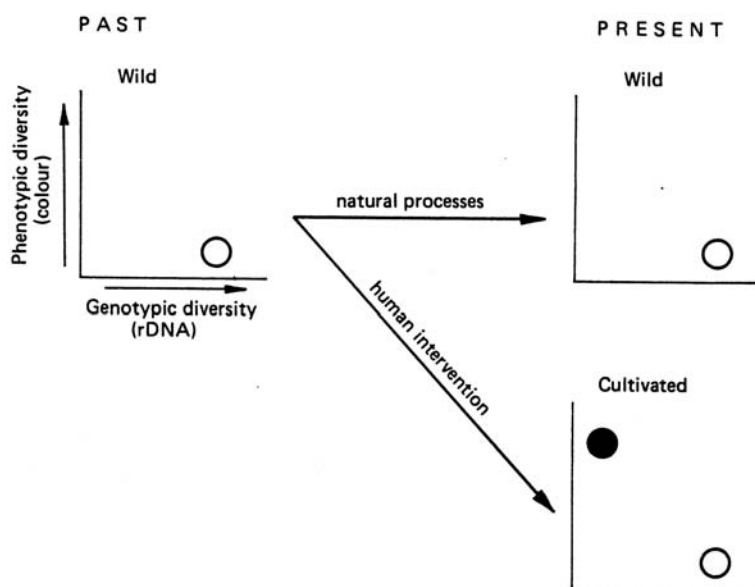


Figure 14.14 Historical model for taro illustrating the origins of an inverse relationship between phenotypic diversity and genotypic diversity, as measured by rDNA analysis. Open circles represent varieties with few anatomical parts (one or less) pigmented with anthocyanins, black circles represent varieties with more than one part pigmented. The model is derived by extrapolating the observations for wild taro in the present to the wild progenitors of cultivated taro in the past. The suggested result of human intervention (selection and propagation) is the creation of a phenotypically diverse but genotypically homogeneous class of highly pigmented, cultivated varieties.

if cultivars with relatively little pigmentation are considered to be primitive (close to wild types), then the detection of rDNA variability might be maximised by sampling primitive varieties from diverse geographical locations.

14.4.5 Ribosomal DNA and chromosome numbers

Ribosomal DNA variants are usually distributed in high copy number at chromosomal loci on one or more homologous pairs (diploids) or triplets (triploids) of chromosomes. Figure 14.15 illustrates, for a hypothetical homologous pair of chromosomes, how both homozygous and heterozygous chromosomes can have homogeneous or heterogeneous rDNA loci. Diploid and triploid plants displaying complex rDNA patterns could be the heterozygous progeny of homozygous diploid parents with homogeneous loci, or they could be the homozygous progeny of heterozygous diploids with heterogeneous loci. Between these two extreme cases, many other possibilities can be imagined.

In situ analysis of the diploid variety AKL 34 (Chapter Twelve) detected two rDNA loci, presumably one per haploid complement (i.e., on one pair of chromosomes). In other diploid and triploid taro, the number of loci per haploid complement may vary, contributing to the range and complexity of rDNA patterns observed. In *Triticum* spp

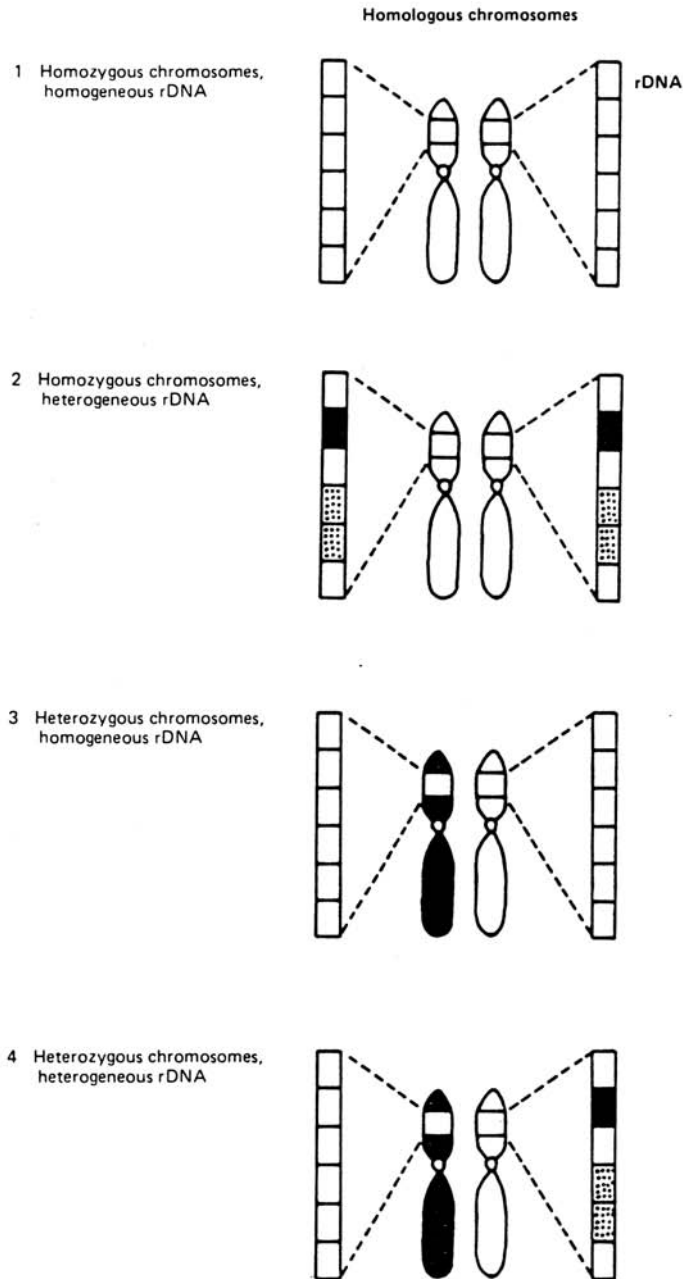


Figure 14.15 Diagram illustrating the distribution of rDNA repeat units on homologous chromosomes (four possibilities). A single rDNA locus is shown on each chromosome. Within rDNA loci, repeat unit variants are indicated as black, grey, or white. This diagram illustrates variation of just two homologous chromosomes, as would be found in a diploid plant, but essentially the same possibilities exist for triploid plants. Homologous chromosome pairs other than those bearing the rDNA loci may be heterozygous or homozygous, and there may be rDNA loci on more than one pair of homologous chromosomes.

(wheat) two or three loci per haploid complement have been recorded (Dvořák 1989). In *Triticum* and *Hordeum* (oats), homogeneity of rDNA spacer lengths within a locus is the prevalent pattern, but in several plant species, *Vicia faba* for example, intra-locus heterogeneity in spacer lengths is also evident. These examples show that for taro, no assumptions can be made about how the rDNA patterns relate to chromosomal homozygosity and heterozygosity, or to intra-locus homogeneity and heterogeneity. Studies of chromosomal morphology provide evidence for structural homozygosity and heterozygosity in taro (Coates et al. 1988), but such variation cannot be directly correlated with rDNA variation without further efforts to identify the chromosomes bearing rDNA loci.

Triploids can be assumed to be entirely or predominantly sterile. If offspring are produced, then these are not necessarily also triploid, because gametes produced by triploids may be haploid, diploid, or aneuploid. The natural dispersal of triploids is therefore limited to vegetative growth and the dispersal of vegetative parts by fresh water. In order to become widely distributed and common in Asia, as observed by Yen and Wheeler (1968) and others, triploids must have been transported by humans, and such dispersal was probably largely an agricultural phenomenon.

The surveys of rDNA in the New Zealand triploids (Chapter Eleven) and in *C. esculenta* var. *fontanesii* (this chapter) indicate that rDNA is stable within clonal lineages. The dispersal of what is believed to be one rDNA variant throughout Queensland must have taken much more than 220 years, the period since taro was first recorded in Queensland by Joseph Banks (see Chapter Nine). The diploid taro in Queensland probably dispersed by vegetative and sexual reproduction, indicating that rDNA in taro is stable over long periods involving sexual generations. Nevertheless, opportunities for rDNA mutation must be greater when both sexual and vegetative reproduction are possible. Most rDNA variants in taro may have originated over a very long period, in the course of vegetative and sexual reproduction by naturally occurring diploids. Ribosomal DNA variants in triploids today could have been inherited, in most cases, from diploid populations with much longer genetic histories than the triploids.

In theory, humans could have produced the present distribution of triploid plants by vegetative propagation of just one triploid clone, but it is unlikely that all rDNA variation in triploids is due to mutation within clonal lineages within the period of agricultural propagation and dispersal of triploids. The best evidence for separate polyploidisation events in the past would be the experimental reconstruction, by breeding, of the different triploids, using diploid varieties with the same range of rDNA variants as found in the triploids. Identifying triploid rDNA variants in diploids would in itself provide good circumstantial evidence for the parentage of triploids.

In the discussion that follows, comparisons of rDNA patterns and historical records are used to interpret the origins of New Zealand and Japanese triploid taro and the recent dispersal history of the triploid *C. esculenta* var. *fontanesii*.

14.4.6 The origins of New Zealand and Japanese triploid taro

Triploid taro were first reported in New Zealand by Yen and Wheeler (1968), and three

phenotypically distinct triploid varieties were described in detail by Matthews (1984, 1985). Two varieties, RR and GR, are common garden varieties, phenotypically very similar (rounded leaves, starchy corms and side-corms), and distinguished only by petiole colour. Var. GP possesses a distinct phenotype, including poor food qualities and long stolons, and is generally found wild. Variation in chromosomal morphology is correlated with the phenotypic variation: varieties RR and GR display cytotype II-3 and are distinct from var. GP, which displays cytotype I-3 (Coates et al. 1988, and Gaffey pers. comm. 1988). Ribosomal DNA variation detected with *Taq* I (Chapter Eleven, Figure 11.9), and *Rsa* I (Figures 11.10, 14.9) is also correlated with the phenotypic variation: varieties RR and GR display the same pattern of rDNA fragments and are distinct from var. GP.

The New Zealand triploid varieties RR and GR produce *Rsa* I rDNA spacer fragments similar to those in four Japanese accessions, T298, 229, 302, and 306 (Figure 14.9). These accessions display rDNA class C, as defined with *Taq* I and *Rsa* I (Figure 14.8). Accessions T298, 299, and 306 belong to the botanical group *Eguimo* (T. Kawahara pers. comm. 1985), one of the fourteen botanical groups of *C. antiquorum* (= *C. esculenta*) described for Japan by Kumazawa et al. (1956). The ribosomal DNA analyses (Figure 14.8) suggest that T302 and T326 (var. *Ishikawa-wase*) also belong to the *Eguimo* group. The growth habit and colouring of the New Zealand triploid var. RR (Figure 5.2), is very similar to that recorded for *Eguimo* in Table 14.8.

The *Eguimo* group is described by Takayanagi (1986) as triploid, and a chromosome count of $2n = 42$ has been recorded for T299 (T. Kawahara, pers. comm. 1985). Matsuda (1950, cited by Yoshitake 1986) examined the morphology and growth of 205 taro varieties (158 from Japan, 38 from Taiwan, seven from China, one from Korea, and one from Sulawesi), and described 22 varietal groups, 15 of which were recognised as old or native Japanese groups. Six of these groups, *Eguimo* among them, included varieties that appear identical to varieties from China or Taiwan. Kumazawa et al. (1956) revised the classification of Matsuda (1950), retaining a similar number of varietal groups, including the *Eguimo* group. Takayanagi (1986, citing Kumazawa 1956) reviewed historical records for varietal names within each of the groups recognised in 1956. The earliest record for the use of the name *Eguimo* in Japan is in the late 17th century. A synonym, *Ao-imo*, was also recorded in Japan in the late 17th century, and in China in AD 560 (Chia, Ssu-hsieh, 6th century, cited by Takayanagi 1986). The historical records are thus consistent with the botanical observation that varieties of the *Eguimo* group are present in China. Varieties in this and other varietal groups are generally believed to be introductions from China. Takayanagi (1986) notes that introductions of taro to Japan could have taken place many different times, and that it is unclear exactly when and how introductions took place.³⁾

Kotani (1981) has reviewed evidence for early plant use in Japan, during the Jomon era of approximately 7000 BP–2300 BP. Nakao (1966, 1967; cited by Kotani 1981) proposed what has become known as the luciphyllous forest hypothesis, which suggests that slash-and-burn agriculture (shifting agriculture) evolved during the Jomon era in the evergreen broad leaf forests of western Japan. Five stages are proposed for the utilisation of plant resources (from earliest to most recent): (1) the gathering of wild nuts and roots,

(2) the selection and improvement of edible species, (3) cultivation of various root crop species, including taro, using slash-and-burn techniques, (4) cultivation of various seed crop species, including rice, with slash-and-burn techniques, and finally (5) wet rice agriculture, associated with irrigation and permanent paddy fields. Kotani (1981) noted that despite the popularity of this hypothesis for many years, no root crop remains had been recovered from the Jomon cultural context, and no convincing evidence for the practice of shifting agriculture had been obtained. Sasaki (1986; cited by Yoshitake 1986) has recently suggested that triploid taro varieties, being more temperate adapted, were introduced to Japan via the Yangtze River, and that diploid varieties may have entered on a warmer route, from Taiwan via the Ryukyu Islands. Sasaki (1986) estimates the date of the first introduction of taro to Japan as approximately 2500 BP, late in the Jomon era (the details of Sasaki's argument are not known to the present author). Yoshitake (1986) notes that taro varieties found in Japan today are not necessarily the same as the earliest introductions.

Yen and Wheeler (1968) recorded no triploid taro in tropical Polynesia, commonly accepted as the area of origin for the Māori. The absence of triploids in this area has been confirmed by later surveys (Sakamoto et al. 1976; Coates et al. 1988). The nearest field location of triploid taro recorded outside New Zealand has been New Caledonia (Yen and Wheeler 1968). The possibility that triploid taro were introduced from Melanesia to New Zealand in prehistoric times was (Yen and Wheeler 1968) and still is (Matthews 1985) contentious. Yen and Wheeler (1968) noted that 'with the wanderings of traders and whalers who took on native crew members in the nineteenth and twentieth centuries, the possibilities of plant transfers, while difficult to document, must be recognised'. They also reported the claim of a Chinese market gardener that a variety then grown in Auckland was imported from China. Morphologically, as judged by experimental cultivation, the market garden specimen was identical with two specimens of taro from near Māori settlements in North Auckland and the Bay of Plenty, and all three possessed similar chromosome numbers (presumably triploid, not directly stated). It was suggested that Chinese taro were imported in the period from the turn of the century until the 1930s by merchants supplying immigrant market gardeners.

The ribosomal DNA comparison, and the historical and botanical records for Japanese and Chinese taro, support the proposition by Yen and Wheeler (1968) that New Zealand triploid taro were introduced from China. The evidence is not proof because triploid taro are widespread in mainland Asia and varieties belonging to the *Eguimo* group may have existed in countries other than China at the time of introduction to New Zealand. It is also quite possible, given the close similarity of varieties RR and GR, that one of these is a colour variant of the other arising by vegetative mutation before or after introduction to New Zealand. Yen and Wheeler (1968) noted that Indochinese (Tonkin) migrants to New Caledonia could have introduced triploid taro to that country. It is likely that many taro varieties are shared by China and neighbouring Indo-Chinese countries.

Migration from the French colonies in Indochina to the colony in New Caledonia predates the turn of the century, and introductions from New Caledonia to New Zealand could have been made in the late nineteenth or early twentieth century. However, New

Zealand trade links with New Caledonia in this period were probably not as strong as with China, and the proposition of a Chinese origin for New Zealand taro (varieties RR and GR) is favoured here. In the absence of any strong affinities with taro outside New Zealand, no suggestions are made here regarding the origin of triploid variety GP.

Accepting that New Zealand triploid varieties originated in China has important implications for taro cultivation in New Zealand. There is no doubt that taro were present in New Zealand in prehistoric times, because of Māori traditions and botanical observations by early European observers (Best 1976). Assuming that the triploid variety GP is also a recent introduction, pre-European taro were probably all diploid varieties introduced from Polynesia. These appear to have been rapidly and almost completely displaced by the triploid varieties, RR and GR, within the last two hundred years. Only two of the nine plants reported by Yen and Wheeler (1968) were diploid. Matthews (1985) found diploid varieties at two sites and triploid varieties (RR, GR) at 193 sites.

Various contributing factors can be suggested to explain the apparently rapid displacement of diploid cultivars: Chinese triploid taro are probably temperate adapted and are probably easier to maintain in New Zealand than tropical Polynesian cultivars. Trials of Polynesian and Melanesian varieties have shown that the tropical varieties do not grow well in Japan, compared with Japanese varieties (Takayanagi 1986). In Japan the climate is temperate and strongly seasonal, as it is in New Zealand. Social factors are also important. Although agriculture has been dominated by European commercial crop species during the last two centuries, the tradition of taro cultivation has survived in Māori communities. Matthews (1985) suggested that the near absence of diploid taro in New Zealand was because of insufficient sampling or because Polynesian diploids were obligate cultivars in the temperate climate of New Zealand. The latter explanation is now favoured.

14.4.7 Widely distributed rDNA classes

The few but widely distributed records of the Col 3:4 and Puk 2:3 rDNA classes are difficult to interpret, since similar rDNA patterns could have been independently generated by similar diploid parents, among indigenous and/or introduced wild populations, in diverse locations. The observations permit the general suggestion that the clones tested, and/or their progenitors, are widely distributed in Asia and the Pacific, but do not allow close historical connections and routes of dispersal by humans to be identified. Better knowledge of geographical distribution, and closer characterisation of the rDNA variants represented in each rDNA class, would remove the problem of possible polyphyletism and strengthen arguments for particular historical connections and dispersal routes.

Ribosomal DNA variants can be monophyletic or polyphyletic, as noted previously for the Queensland rDNA variant, and combinations of rDNA variants can also be monophyletic or polyphyletic, depending on whether or not sexual processes (segregation and reassortment, recombination, and less well-known processes) produce the same combination of variants independently in different areas. Useful and not useful genotypic markers are characterised, in theoretical prescriptions, in Table 14.9. These prescriptions

also apply to conventional alleles and combinations of alleles, those characterised by iso-enzyme analysis for example.

The Col 3:4 and Puk 2:3 classes are probably monophyletic in some sense (Table 14.9, A1 to A6), but without closer analyses it cannot be assumed with complete certainty that they are not polyphyletic combinations of polyphyletic variants (Table 14.9, B2). In the case of *C. esculenta* var. *fontanesii*, discussed next, available historical records, and the fact that this variety is triploid, support the suggestion that the samples examined possess a monophyletic combination of rDNA variants (Table 14.9, A2, A3, or A4).

Examples of *C. esculenta* var. *fontanesii* from Sri Lanka (wild), New Zealand (cultivated ornamental) and Australia (cultivated ornamental) displayed identical phenotypes and rDNA patterns (Eli 3:5 class). Engler and Krause (1920) noted that var. *fontanesii* had been cultivated for a long time in hothouses in Europe, and according to Schott (cited by Engler and Krause 1920) it was cultivated in Holland around 1680 or 1690 as '*Arum Colocasia*' or '*zeylanicum*', and the latter name suggests that the variety was introduced to Europe from Sri Lanka (formerly Ceylon). Because Australia and New Zealand were colonised primarily by Europeans, in the recent historical period, it is likely that var. *fontanesii* was introduced to these countries directly from Europe rather than from Sri Lanka. However, if the variety is also widespread in Asia in cultivation or in the wild, then it might well have been introduced directly from Asia. So far the variety has only been recorded in Sri Lanka. If it was not further introduced to Europe from Asia after 1690, and if Europe really was the source of the New Zealand and Australian examples, then the rDNA variants represented by the class Eli 3:5 must have existed for at least 300 years, following the 1690 date for Holland. Chromosome counts for plants from Sri Lanka and Australia show the variety to be triploid, so it is probably fully or mostly sterile. The phenotype and ribosomal DNA of var. *fontanesii* have probably been stable for at least 300 years of vegetative propagation as an ornamental (Figure 14.16 illustrates the historical reconstruction). Examples of var. *fontanesii* in Europe today are predicted to be identical to the plants recorded here for Sri Lanka, Australia, and New Zealand.

Table 14.9 Prescriptions for genotypic markers (rDNA complements) for investigating dispersal history.

Useful	
A1	Monophyletic variant
A2	Monophyletic combination of monophyletic variants
A3	Monophyletic combination of polyphyletic variants
A4	Monophyletic combination of monophyletic and polyphyletic variants
A5	Polyphyletic combination of monophyletic variants
A6	Polyphyletic combination of monophyletic and polyphyletic variants
Not useful	
B1	Polyphyletic variant
B2	Polyphyletic combination of polyphyletic variants

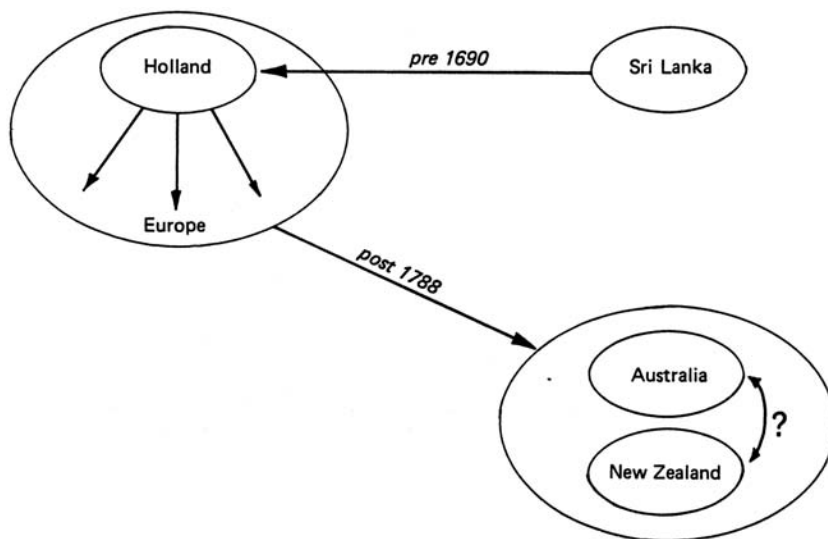


Figure 14.16 The possible recent origins of *C. esculenta* var. *fontanesii* in Australia and New Zealand. In both countries, it is now cultivated as an ornamental.

If the triploid var. *fontanesii* is indigenous to Sri Lanka, then diploid descendents of its diploid progenitors might exist there now. Distinctive phenotypic qualities of var. *fontanesii* (very shiny, leathery leaves, see Figure 10.2) have not been noted among any cultivated taro from Asia and the Pacific. The nearest diploid relatives of var. *fontanesii* may be genetically isolated in some way, perhaps because of a geographically isolated or very localised distribution.⁴⁾

14.4.7 Concluding statements

The present, non-intensive analysis of rDNA, with few restriction enzymes, appears better suited to locally intensive geographical surveys than to comparisons between few samples separated by very large geographical distances. Further intensive characterisation of the Queensland rDNA variant is recommended because this may be an ancient variant within the species, and may also be characteristic for taro in the tropical region of Asia and the Pacific.⁵⁾

Notes

- 1) This variety has been recognised as a member of the Egu-imo Group (Takeshita et al. 1991)
- 2) Heterozygosity and breeding at a Queensland taro site were recently demonstrated by Hunt et al. (2013), using samples collected during the 1987 field survey.
- 3) Further characterisation of rDNA variation in Japanese taro varieties was carried out by Matthews, Matsushita et al. (1992). Matsuda (2002), and Matsuda and Nawata (2002),

extended the rDNA survey into China and northern Vietnam, and suggested that most Japanese cultivars are derived from common Chinese cultivars.

- 4) A contrary interpretation is now possible: The wild species *Colocasia lihengiae* (Long and Liu 2001) has shiny, leathery leaves that are distinctly angular in outline, and was recently found in Arunachal Pradesh, India (Gogoi and Borah 2013) (shiny leaves indicate a lack of waxy leaf hairs; the leaves of *C. esculenta* are mainly dull in appearance because of waxy hairs that repel water). The widespread *C. lihengiae* might have crossed – in India or elsewhere – with *C. esculenta*, leading to production of var. *fontanesii* as a polyploid hybrid. This speculative suggestion can be tested through genetic analysis.
- 5) Matroud et al. (2012) have described a nested tandem repeat (NTR) structure present in large intergenic spacer region of taro rDNA. Their preliminary analysis suggests that changes in the NTRs of taro have been occurring on a 1000 year time scale, and that analysis of NTRs may be useful for studying plant populations.

Chapter Fifteen

Origins and Antiquity of Diploid Taro in Australia and New Guinea, and Triploid Taro in Asia

The major question raised in Chapter Nine was whether or not taro provided a basis for the indigenous development of agriculture in New Guinea. Taro could have been of ancient natural occurrence in Australia and New Guinea (Sahul), or could have been a pre-agricultural introduction by humans. The distinction is important because pre-agricultural dispersal of taro by humans, to Australia and New Guinea, could have established wild populations that were better or worse material for domestication than natural wild populations elsewhere. The antiquity of taro in Sahul, and the possibilities of natural occurrence versus introduction, were not resolved by the surveys of rDNA variation, but future examination of rDNA and other aspects of genotype could be informative, as discussed in Chapter Fourteen.

In the present chapter, other kinds of biological evidence are discussed with an emphasis on the possible pre-agricultural occurrence of diploid taro in Sahul. Some original field observations are briefly reported, as illustration. In the second part of the chapter, the possible origins and antiquity of triploid taro in Asia are discussed.

15.1 Diploid Taro in Australia and New Guinea (Sahul)

15.1.1 Archaeological and natural fossil remains

The soft herbaceous parts of taro are not very likely to be preserved as fossils, although they could be preserved in waterlogged swamp sites or as impressions in volcanic deposits (Spriggs 1982). Fossil taro seed have not been reported, and although pollen have been identified in archaeological sites in New Guinea, the identifications are not considered secure (Spriggs 1982). Charred remnants of taro, the outcome of cooking, may be a more likely source of archaeological fossils. The taxonomic characterisation of charred root crop remains is in progress (Hather 1991).

The possibility of recovering taro seed from archaeological contexts is indicated by the production of abundant seed in taro fruit (Figure 9.3). The general rarity of flowering within cultivations today suggests that pollen is unlikely to be found in the archaeological remains of cultivations (Spriggs 1982). A palynological analysis of deposits from a currently cultivated taro pond-field on Futuna did not reveal taro pollen because of the lack of flowering and/or because taro pollen did not survive the recovery techniques used (A. di Piazza, S. Haberle, pers. comm. 1989). In Australia, flowering by wild taro is common in Queensland (P. J. Matthews, field notes, and R. Hinxman, pers. comm. 1987). This area provides opportunities for testing recovery techniques in sites where pollen is

known to be produced, unrestrained by human actions. Direct observations of pollen deposition and initial degradation or preservation would be useful for assessing pollen recovery from archaeological deposits. Ancient natural sediments in Queensland are a potential source of direct evidence for the pre-human or pre-agricultural antiquity of taro in Sahul, and are perhaps more accessible than suitable deposits in New Guinea.¹⁾

Starch grains and calcium oxalate raphides have been discovered on stone tools from the Solomon Islands, dating from 28,000–20,000 BP (Loy et al. 1992). After comparisons with the morphology of contemporary starch- and raphide-producing genera and species, the archaeological remains have been interpreted as probably coming from *Colocasia esculenta* and *Alocasia*. The evidence does not indicate whether cultivated or wild plant sources were involved, and sheds no light on whether or not taro is indigenous to the Solomon Islands. Fossil remains from a pre-human context are needed for direct proof that taro is indigenous. Nevertheless, if the interpretations are correct, the archaeological observations are the first direct evidence for taro in any part of Asia or the Pacific, much earlier than any date recorded for agriculture.

Spriggs (1982) noted the possibility of archaeological preservation of insects associated specifically with taro, giving *Papuana* spp. (taro beetles) and *Tarophagus proserpina* (taro leaf hopper) as examples. Whether or not these insect species are associated exclusively with *C. esculenta* is not yet clear. In the following discussion of insects associated with taro, the need to investigate host specificity is emphasised. It is an issue with double significance — for interpreting the evolutionary history of taro, and for interpreting archaeological remains of insects associated with taro.

15.1.2 Organisms that require taro as a host

A biological approach to estimating the antiquity of taro in Sahul can be made by examining organisms that require taro as a host. Endemic differentiation of organisms associated with taro in Sahul might suggest pre-human antiquity for taro, regardless of whether or not taro itself underwent endemic differentiation. The suggestion is qualified here, because taro could have been introduced as long ago as 40,000 years, and differentiation of an associated organism might have occurred within this period. Exploring this last possibility is beyond the scope of the discussion that follows.

Drosophilid flies

During fieldwork by the present author, drosophilid flies were found swarming in and around inflorescences of wild taro alongside a coastal forest stream between Lae and Salamaua in Morobe Province, Papua New Guinea, in July 1985 (Figure 15.1). Specimens taken from within an inflorescence were later identified by M. Arura (PNG Department of Primary Industries, Bubia) as *Drosophilella* (syn. *Colocasiomyia*) *pistilicola* Carson and Okada (Diptera: Drosophilidae)²⁾. This and another species, *Colocasiomyia stamenicola* Carson and Okada (1980), were first described by Carson and Okada after collecting flies in approximately the same area in the period August to December 1977. These workers investigated the ecology of drosophilid flies in this area, and examined numerous species associated with a wide range of plants. Their conclusions

regarding the specific association of drosophilid flies with flowers of *C. esculenta* are thus highly significant. Carson and Okada (1980: 28) write:

The inflorescence of *Colocasia esculenta* is a complex microcosm with four members of the family Drosophilidae of three genera breeding in it in the Morobe District of Papua New Guinea. The most thoroughly adapted for life in this specific type of inflorescence are the two species of *Drosophilella* [syn. *Colocasiomyia*]. Large number of adults of both species enter the fresh flower just as it is opening...these two species share the inflorescence niche in an extraordinarily precise manner. This reflects a set of highly refined adaptations in the case of the *Drosophilella* species; indeed, these species are apparently highly restricted to their host plant, *Colocasia esculenta*. As will be reported in a later paper...they do not visit even the quite similar inflorescences of other species of Araceae growing in very close proximity of *Colocasia*.... Although there are very strong similarities between *D. stamencicola* and *D. pistilicola*, they should not be described as



Figure 15.1 *Colocasiomyia* on a spathe of wild taro in Morobe Province, Papua New Guinea, July 1985. The flies shown may include both *C. pistilicola* and *C. stamencicola*. (This plant was growing on the bank of a stream, in a forest, opposite the plants shown in Figure 10.9).

sibling species. Any one of a number of specific morphological differences can be used to separate them. Furthermore, strong morphological similarities are found between *stamenicola* and *alocasiae* and between *pistilicola* and *colocasiae*. The systematic and ecological relationships of these new species to others found in closely related hosts should serve as an interesting topic for further study.... Further investigation of the insect associates of *Colocasia esculenta* may aid in an estimation of the ancestral home of this important food plant.

If particular species of *Colocasiomyia* are associated exclusively with taro and are endemic in Papua New Guinea, then the degree and nature of endemic differentiation by the insect species might provide circumstantial evidence for taro being indigenous. The available evidence for *Colocasiomyia* from within and beyond Papua New Guinea does in fact suggest that this is the case, as follows.

C. pistilicola and *C. stamenicola* breed microallopatrically on the same spadix of *C. esculenta* in Papua New Guinea (Carson and Okada 1980). The microallopatry is exhibited by the larval life stages of these species, with larvae of *C. pistilicola* occupying the pistillate (female flower) zone within the taro inflorescence, and larvae of *C. stamenicola* occupying the staminate (male flower) zone. These species are described by Carson and Okada (1982a) as 'synhospitalic', a term indicating the occurrence of two or more related parasitic species on the same host species or individual. Two other species, *C. xenalocasiae* Okada 1980 and *C. alocasiae* Okada 1975, share the spadix of *Alocasia odora* C. Koch in Taiwan and Okinawa (Okada 1975; Carson and Okada 1982a: 14). The phyletic relationships among these four *Colocasiomyia* species were analysed taximetrically using twenty diagnostic characters (Okada 1980). The analysis shows that *C. pistilicola*, the pistillate species on *Colocasia* in Papua New Guinea, is very similar to *C. xenalocasiae*, the pistillate species on *Alocasia* in Taiwan. In a reciprocal manner, *C. stamenicola*, on *Colocasia* in Papua New Guinea, closely matches *C. alocasiae*, its staminate counterpart on *Alocasia* in Taiwan. A fifth species has been described, *C. colocasiae* Duda 1924 from Java, collected from *C. esculenta* (Okada 1981: 279). From limited information (not all characters could be observed), this species is interpreted as being closest to *C. pistilicola* (Carson and Okada 1982a). Okada (1980) makes the prediction that another species will be found in Java which is synhospitalic with *C. colocasiae* and closely related to *C. stamenicola*. Carson and Okada (1982a: 14) suggest the following evolutionary scheme:

It may be supposed that a couple of ancestral species of *Drosophilella* [syn. *Colocasiomyia*] had established synhospitalism on some plant of Araceae in a certain area of the Oriental Region, probably the southern part of Angaraland (mainland Asia). Tightly keeping synhospitalism, they then evolved into *alocasiae* and *xenalocasiae* and dispersed in the direction of Taiwan and Okinawa on the one hand and into *colocasiae* and an unknown species in Java as well as into *stamenicola* and *pistilicola* in New Guinea in a more easterly direction. The process of synhospitalic evolution and dispersal of *Drosophilella* probably retained an intimate association with the evolution and dispersal of

the host plants. Furthermore, the process might well be correlated with land elevation in the southern islands through eustatic movement of the sea level during the early Neogene. Establishment of the present status of the distribution of these species was probably not much concerned with vicariance of primarily widely distributed ancestral species.... Rather, this case appears to have a more simple dispersal from a certain center of origin towards geologically newer lands.

Carson and Okada (1982a) thus suggest that the differentiation and dispersal of *Colocasiomyia* species was linked with the differentiation and dispersal of *Alocasia* and *Colocasia* species at a time which corresponds to the Miocene convergence (Whitmore 1981) of Laurasia and Gondwanaland. Little is known about the rate, degree, and location of genotypic differentiation in the insect and host species, and it cannot be assumed that the postulated evolutionary processes required as much as the 20–25 million years since the early Neocene. Jackson and Pelomo (1980) report that *Colocasiomyia* sp. nr. *seminigra* Duda is often present in large numbers in taro flowers in the Solomon Islands. The observation raises several questions. For example, do endemic *Colocasiomyia* species exist in the Solomon Islands? Do *Colocasiomyia* species occur any further eastwards, on remote oceanic islands? Such occurrences would suggest that the insect is an associate of human dispersal of taro.

Investigations of insects associated with *A. brisbanensis* Hay and *C. esculenta* in Australia would help to illuminate the evolutionary history of associations between drosophilid flies and taro. Although *Colocasiomyia* species have not been reported in Australia (Bock 1982), species of other drosophilid genera, *Drosophila* and *Styloptera*, have been³. Specimens of *Drosophila specensis* Bock, examined by Bock (1976), were not accompanied by information on particular plant hosts, but the species was clearly associated with rainforest habitats over a wide range within northeast Queensland. It may well be associated with *A. brisbanensis* and/or *C. esculenta* in this region, since another species of *Drosophila*, *D. metatarsalis* Okada and Carson, is associated with *Alocasia* and *Colocasia* in Papua New Guinea. *D. metatarsalis* was described for the first time after being collected from *A. macrorrhizos* (*A. nicolsonii* Hay, Hay pers. comm. 1989) and *C. esculenta* in Morobe Province, Papua New Guinea. Most examples found by Okada and Carson (1980) were in or near inflorescences of *A. nicolsonii*, but one female was reared from an inflorescence of *C. esculenta*. The authors noted that *D. metatarsalis* resembles *D. specensis* Bock 1976 from Queensland, Australia.

Two new species of *Styloptera* Duda were described by Okada and Carson (1980) and Carson and Okada (1980) from collections made in Morobe Province in 1977. One of these, *S. alocasiae* Okada and Carson, was found only on *Alocasia* spp., and the other species, *S. repletoides* Carson and Okada, was found only on *C. esculenta*. Apart from *S. formosae* Duda, recorded in Taiwan, only two other species of *Styloptera* are known, *S. striata* Bock and *S. wheeleri* Bock. Both are Australian and are known from one site each in northeast Queensland, within the known range of wild *C. esculenta* and *A. brisbanensis*. The 1967 collection site for *S. styloptera* (Bock 1982) was a waterfall location known as The Boulders (site 9 in Figure 14.3), where wild taro was collected in

1987. If, as seems quite likely, *Styloptera* spp. are specifically associated with taro in Papua New Guinea and Australia, and the insect species are endemic within Sahul, then this would support the suggestion that taro is indigenous to Sahul.

The insect associations of *Colocasia* and similar aroid hosts, notably *Alocasia* spp., represent a barely touched field of investigation. Okada and Carson (1980) describe, on the basis of collections within one small area of Morobe Province, Papua New Guinea, fourteen new species of Drosophilidae associated with the flowers of *A. macrorrhizos* (*A. nicolsonii* Hay?). This plant was described by Carson and Okada (1982b: 682) as a 'veritable zoological garden' for drosophilids. Studies of *A. brisbanensis* in Australia show that the garden of *Alocasia* contains more than just drosophilids. *Neurochaeta inversa* McAlpine is a new genus and new family (Neurochaetidae) known only in association with *A. macrorrhizos* (i.e. *A. brisbanensis* Hay), in or near rainforest habitats (McAlpine 1978; Shaw and Cantrell 1983a). Insects from families Aphididae, Ceratopgonidae, Chloropidae, Formicidae, Muscidae, Nitidulidae, Phoridae, and Staphylinidae were also observed on *A. macrorrhizos* (i.e. *A. brisbanensis* Hay), in Australia (McAlpine 1978; Shaw et al. 1982; Shaw and Cantrell 1983b). These associations may or may not be host specific.

Less is known about insects associated with wild taro in Australia. During fieldwork in Queensland in September 1987, no drosophilids were seen on inflorescences. However, flowering in Queensland spans at least seven months, from September (personal observation 1987) to March (Hinxman pers. comm. 1989), and drosophilids might only become apparent at a certain time within this period.

Delphacid planthoppers and viruses

Adult specimens of *Tarophagus colocasiae* Matsumura (stat. rev. and comb. n. Asche and Wilson 1989) (Homoptera: family Delphacidae) were collected by the present author in September 1987 from the leaves of wild taro at Jiyer Cave on the Russell River (site 10, Figure 14.3). The specimens were later identified by Dr J. Donaldson, Queensland Department of Primary Industries, and are the first record of *T. colocasiae* in Australia (Donaldson, pers. comm. 1989)⁴.

A nymph of what may be *Tarophagus* sp. was subsequently found on a plant collected by R. Hinxman approximately 2 km north of Jiyer Cave, at Moochoopa Falls, in August 1989 (Figure 15.2). It is difficult to identify nymphs because the available taxonomic descriptions for *Tarophagus* are based on adult morphology (Donaldson, pers. comm. 2002). The genus *Tarophagus* has been revised, and is recognised as containing three species (Asche and Wilson 1989). The known geographical distributions of these species differ, but overlap in the eastern part of mainland New Guinea (Figure 15.3).

Tarophagus is one of two insect genera known to transmit Alomae and Bobone viruses, which are apparently endemic to Papua New Guinea and the Solomon Islands (Mitchell and Maddison 1983). If these viruses are restricted to taro as a host, then their endemic differentiation in the New Guinea area might support the suggestion that *C. esculenta* is indigenous to New Guinea. Another virus, Dasheen Mosaic Virus (DMV), is

common worldwide among cultivated aroids (Zettler and Hartman 1986), and has been reported for cultivated aroids and wild *Alocasia* in Queensland (Greber and Shaw 1986). The spread or otherwise of virus diseases between wild *Alocasia* and *Colocasia* in Queensland would provide a measure of the host specificity of insects associated with taro. If any viruses are associated specifically with wild taro in Australia, then their

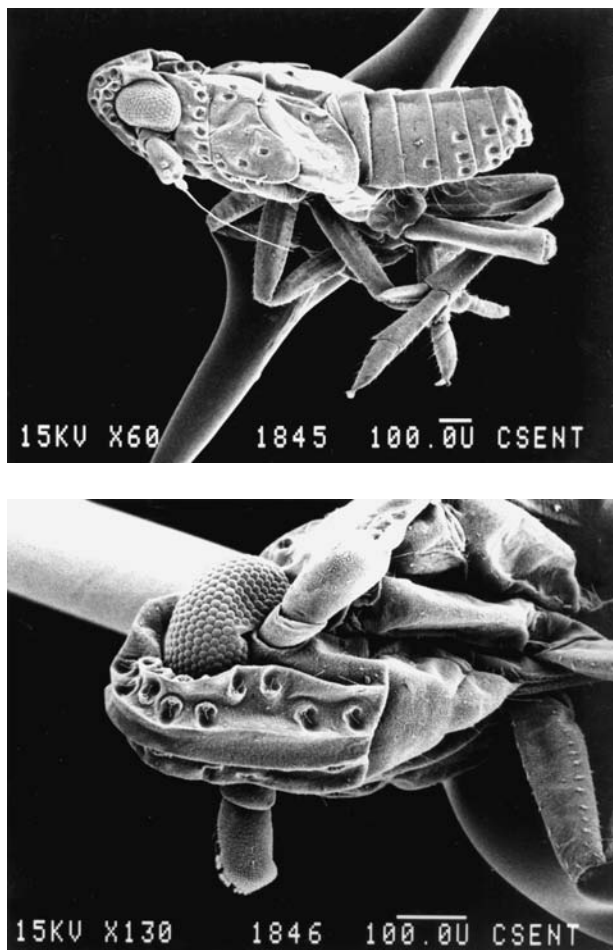


Figure 15.2 Nymph from a leaf of wild taro collected by R. Hinxman, 8 October 1989, in rainforest at Moochoopa Falls, Bellenden Ker National Park, Northeast Queensland. Tentatively identified as *Tarophagus* Zimmerman (Asche and Wilson 1989), species not determined. Upper photo: view of entire insect. Lower photo: front of head. Scale bars 100 μ m (0.1 mm) in both photos. The antennae, head structure, number of abdominal plates, and the foliate spur on the rearmost leg appear the same as shown for the adult stage of *Tarophagus*, described by Asche and Wilson (1989). Photographed with a Joebel scanning electron microscope, by D. Rentz, Department of Entomology, C.S.I.R.O., Canberra.

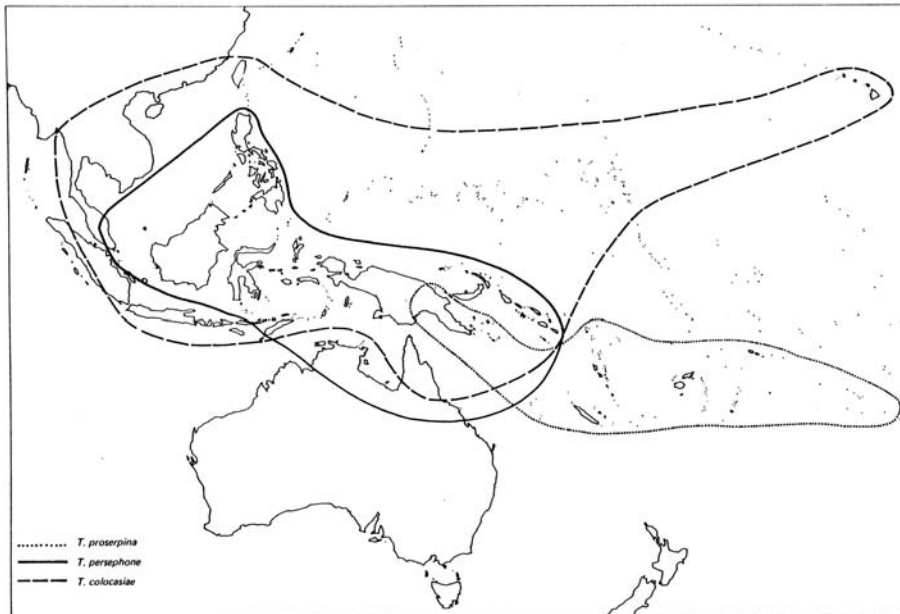


Figure 15.3 *Tarophagus* species in Southeast Asia and the Pacific. Adapted from Asche and Wilson (1989) with the addition of one record (collection by author) of *T. colocasiae* in Queensland.

distribution and differentiation within Australia would have significance for the possible origins of Australian taro.

Mitchell and Maddison (1983) noted *Alocasia* spp. as alternative hosts for *Tarophagus proserpina* (information source not given), but no distinction was made at that time between the three species of *Tarophagus* recognised now. It is therefore still possible that one or two species of *Tarophagus* are associated with *C. esculenta* exclusively. The only information available regarding *Alocasia* as an alternative host is the unsourced comment by Mitchell and Maddison (1983), and it is only implied by Asche and Wilson (1989) that all three species of *Tarophagus* are associated with *C. esculenta*. The host specificity of *Tarophagus* remains an open question. The extensive survey of Asian and Pacific insect records and collections by Asche and Wilson (1989, and Figure 15.3) shows that *T. proserpina* is endemic to the South Pacific. If *T. proserpina* is associated exclusively with taro, this would support the suggestion that taro is indigenous to New Guinea. The distribution of *T. proserpina* is intriguing because it suggests that cultivated taro was dispersed from Melanesia eastwards to Polynesia, but not west to Asia or north to Micronesia. According to Waterhouse and Norris (1987), *Tarophagus* was first established in Hawai'i in 1930, when its population rose and caused major crop damage. Presumably the species involved then was *T. colocasiae*, the only species recorded for Hawai'i by Asche and Wilson (1989). Plant transfer during the last

two centuries may well have increased the range of *T. colocasiae* and *T. proserpina* in the Pacific, but this does not affect the possible prehistorical significance of the absence of *T. proserpina* from Asia.

15.1.3 Lake Carpentaria and land connections between Australia and New Guinea

Taro may have reached Sahul before, during, or after the last period of low sea level, in the late Pleistocene, by natural means or as an introduction by humans. Until more is known about the natural vectors of taro fruit and seed, and the differentiation of taro within and beyond Sahul, it will be impossible to relate the present distribution of wild taro to particular geomorphological episodes. It is nevertheless of interest to consider the possible significance for taro of Lake Carpentaria and adjacent land areas between Australia and New Guinea during the late Pleistocene. During the last period of low sea

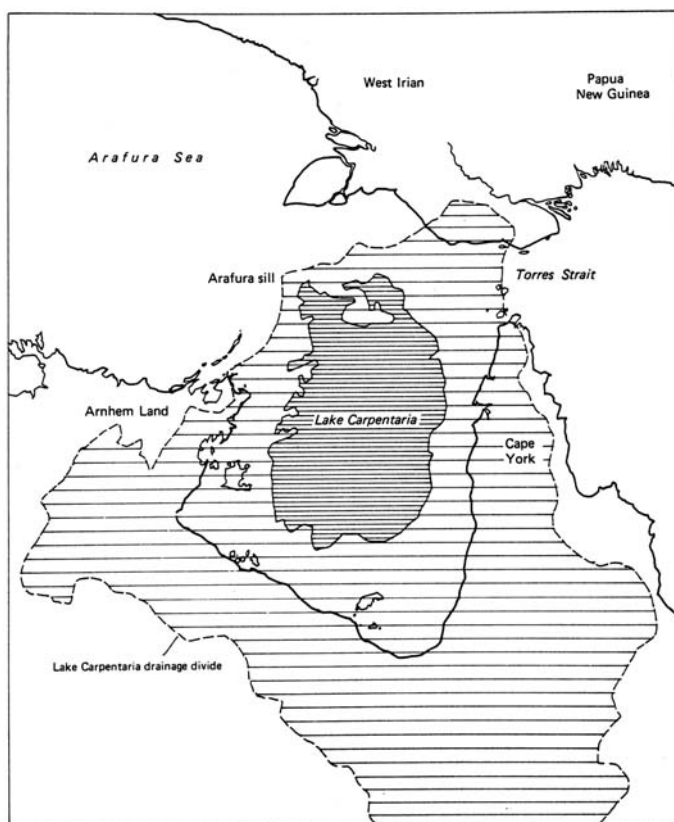


Figure 15.4 The Carpentaria drainage basin showing the maximum extent of Lake Carpentaria Basin, juxtaposed with the present coastlines of Australia and New Guinea. Lake Carpentaria is believed to have existed throughout the period of approximately 35,000 BP to 12,000 BP, with a maximum depth of only 10 m, and fresh-to-brackish water. Adapted from Figure 1a, Torgersen et al. (1988).

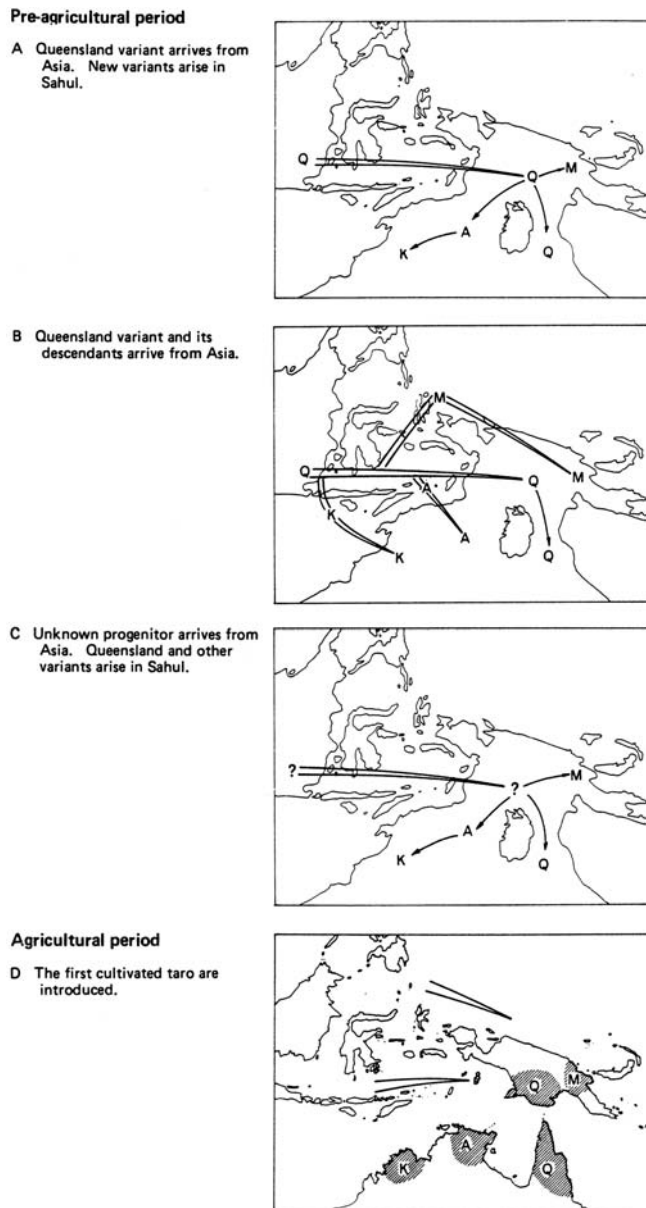


Figure 15.5 Possible origins and dispersal of diploid taros that display different rDNA patterns, in Sahul (panels A-G). Q = Queensland rDNA variant, Qld 1:1 class; K = Kim 2:2 class; A = Arn 2:2 class; M = Morobe Province rDNA patterns, with *Taq* I and *Hinf* I spacer fragments of c.4.6 kbp. The continent of Sahul is shown with Australia and New Guinea connected by land and with Lake Carpentaria, in the pre-agricultural period, before 8,000 years BP. The full separation of Australia and New Guinea by rising sea levels occurred at about 8,000 years BP. Panel D illustrates a possible scenario for the distribution of wild taro, and the possible introduction of cultivated taro from Asia, at an unspecified time after 8,000 BP, in the agricultural period. Agriculture may have begun in New Guinea with the introduction of cultivars from Asia, or it may have begun earlier, with selection from a range of wild taro already present.

level, from approximately 35,000 to 12,000 years BP, three main geographical features lay between Australia and Papua New Guinea: Lake Carpentaria, the Arafura Sill, and the Cape York/Torres Strait landbridge (Torgersen et al. 1988, and Figure 15.4). The shoreline and floodplains around Lake Carpentaria may have been unsuitable for taro if they were alternately subject to wet-season inundation and dry-season drought, as suggested by Torgersen et al. (1988). Permanent water sources suitable for taro may have existed above the floodplains, on the Arafura Sill and along what is now Cape York, and these areas may have provided routes for dispersal between the two sub-continent during the Pleistocene. A route or routes of dispersal might become evident from a detailed survey of genotypic differentiation among wild taro in the areas that once surrounded Lake Carpentaria. Surveys in Wallacea, the island region in central Malesia which lies between Wallace's line and Weber's line (Whitmore 1981), and in adjacent areas of Indonesia west of Wallace's line, are also needed to determine the history of wild taro in Sahul. The same areas would also be of pivotal interest for investigating the insects associated with taro in Sahul.

Scenarios for the origins and dispersal of the Queensland rDNA variant (Qld 1:1 class, Chapter Fourteen) are presented in Figure 15.5, where it is assumed that taro arrived before agriculture began in New Guinea, during an unspecified period of low sea level. It is also assumed that the other rDNA classes recorded for wild taro in Australia and New Guinea are derived from the Queensland rDNA variant. The possible polyphyletic origins of rDNA variants and classes are discussed in Chapter Fourteen. If taro reached Sahul very early, before Australia and New Guinea were fully separated by rising sea levels (c. 8000 BP, Torgersen et al. 1988: 259), then taro with the Queensland rDNA variant may have dispersed north and south of the Carpentaria basin as suggested in Figure 15.5A, B. Figure 15.5C illustrates the possible evolution of the Queensland rDNA variant within Sahul, in Queensland. The locations shown for the origin of the Queensland rDNA variant, Figure 15.5A, B, C, are purely hypothetical in each case. Figure 15.5D shows one of many possible scenarios for the differentiation and distribution of wild taro in Sahul, after the separation of Australia and New Guinea by sea. Cultivated taro are shown as introduced from Asia, but they may have also originated locally, from already existing wild populations, as discussed next.

15.1.4 Origins of cultivated and wild taro in Sahul

Given the various indications that taro reached Australia and Papua New Guinea in ancient times, in the pre-agricultural period, the major question that then arises is whether or not wild taro like those found today were alone sufficient for the evolution of cultivated taro in Papua New Guinea. This question could be addressed by phylogenetic analyses of wild and cultivated taro, using any parts of the nuclear, mitochondrial or chloroplast genomes that are informative for intra-specific phylogeny. Alternatively, the possible derivation of cultivated varieties from local wild populations could be investigated by examining genes (and their products) that directly affect qualities favoured by cultivators. Examples are genes affecting the synthesis and degradation of stored starch, or the production of enzymes such as trypsin inhibitor, which inhibits

digestive enzymes, and thus reduces the digestibility of taro for animals and humans (Bradbury and Holloway 1988: 109).⁵ Wild taro in Australia and Papua New Guinea produce very little starch compared to cultivated or known feral varieties (personal observation).

Whether or not wild taro in Sahul are of pre-agricultural origin remains unresolved. To summarise the discussions here and in the preceding chapter, four general approaches can be suggested for future research: (1) a search for endemism in wild taro genotypes, using typological and phylogenetic analysis, and geographical surveys within and beyond Sahul; (2) a search for evidence of long-term and differential gene flow between wild populations in different parts of Australia and New Guinea; (3) a search for ancient archaeological and natural remains, and (4) investigation of the possible host specificity and endemism of organisms associated with taro.

15.2 Origins and Dispersal of Triploid Taro

15.2.1 Genetic mechanisms that create triploids

Mitotic chromosome doubling in a normal diploid ramet (the separate shoot or branch of a clonal lineage) could produce a tetraploid ramet (Figure 15.6). Vegetative proliferation of such a ramet would create a tetraploid clonal lineage with the potential to flower and produce many diploid (abnormal) gametes by normal meiotic processes. Such a clone could, in theory, produce many tetraploid offspring by self-pollination. This is illustrated in Figure 15.6 by the seedling with a somatic chromosome number of $2n = 56$. Triploid offspring, with a chromosome number of $2n = 42$, could also be produced by cross fertilisation with diploid shoots from the same clone (Figure 15.6), or different clones.

Alternatively, triploid taro might arise after rare, unreduced, diploid gametes were produced by abnormal male or female meiosis, or by aberrant pre-meiotic mitosis within floral cell lineages. Rare unreduced gametes would usually fertilise, or be fertilised by, normal haploid gametes. Tetraploids produced by the combination of rare unreduced gametes would be very rare or absent (Figure 15.7).⁶ This theory is consistent with the absence of tetraploids in chromosome number surveys to date (Yen and Wheeler 1968; Sakamoto et al. 1976; Kuruvilla and Singh 1981; Coates et al. 1988).

From the above discussion it is concluded that sexual reproduction was essential for the creation of triploid varieties of taro, and that most triploids originated in the wild, where sexual reproduction is unrestrained. Pollen is produced by an inflorescence before seed, and cultivated plants are more likely to produce pollen than seed before being harvested. Occasionally, pollen from cultivated taro might be carried to nearby wild plants by species of *Colocasiomyia* (Figure 15.1), drosophilid flies, which are likely pollinators for taro (Carson and Okada 1980). In this way, aberrant sexual processes in cultivars could have led to the production of triploid seedlings in the wild, as suggested in Figure 15.7.

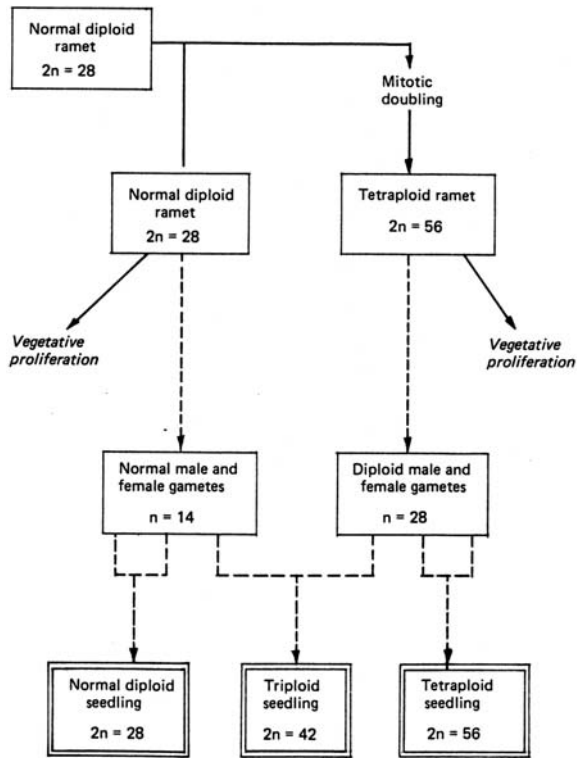


Figure 15.6 Scheme for the production of triploid taro by aberrant vegetative reproduction

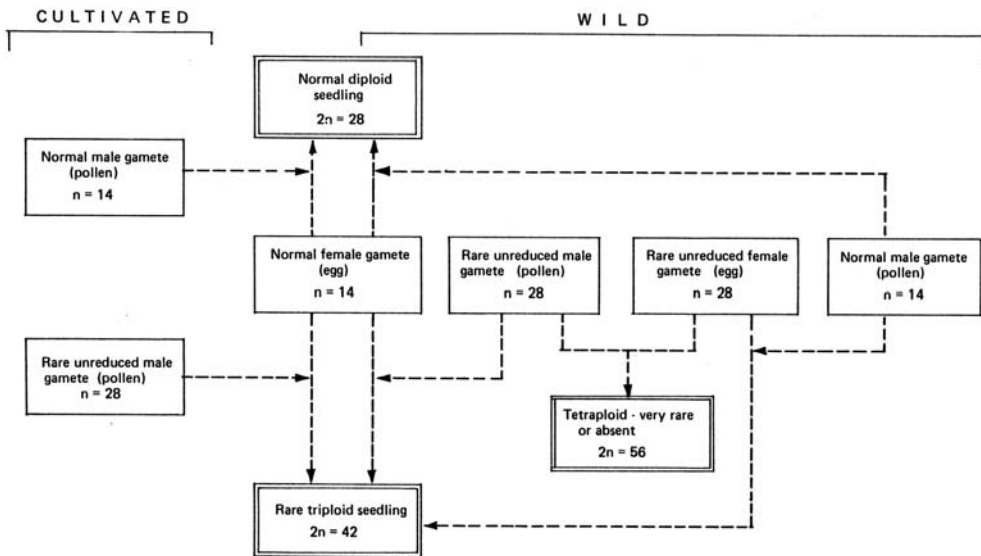


Figure 15.7 Scheme for the production of triploid taro by aberrant sexual reproduction

15.2.2 Evidence for the multiple origins of triploid taro

The multiple origins of triploid taro from different seed are indicated by the accumulated circumstantial evidence for diversity among triploids. Extreme differences in phenotype are exhibited, for example, by the New Zealand triploids var. RR (starchy with side-corms), var. GP (non-starchy with stolons), var. *fontanesii* (extremely dark anthocyanin pigmentation, very waxy leaves, non-starchy with stolons). Ribosomal DNA variation is recorded in Chapter Fourteen, and variation in chromosome morphology has been described by Coates et al. (1988).

Two triploid lineages are recognised by Coates et al. (1988), one characterised by the possession of three sets of acrocentric chromosomes (cytotype II-3) and the other by two sets of metacentric chromosomes with a third set containing metacentric and acrocentric chromosomes (cytotype I-1). The identification of homology between the various metacentric and acrocentric chromosomes is based on entire chromosome lengths and on the ratios of chromosome-arm lengths within each chromosome. In taro, these morphological characters are not very distinctive, and Coates et al. (1988) adopted the simplest possible interpretation by aligning chromosomes in a way that minimised the number of different arrangements recognised among the plants analysed. This reasonable but conservative approach may underestimate variation within the species. In all, eight different combinations of rDNA variants have been recorded for triploids in tests with *Taq* I, *Hinf* I, and *Rsa* I: two from New Zealand (Figures 11.9, 11.10, 14.10), three from Japan (Figures 14.8, 14.9), two from Nepal (Appendix 20) and one from Sri Lanka (Figure 14.11). As noted in Chapter Fourteen, proof that the different triploid lineages have separate sexual origins requires the identification of diploid progenitor genotypes (see Briggs and Walters 1984: 216–47 for some discussion of methods for identifying the progenitors of polyploids). For the purposes of further discussion, I will assume that triploid clones of taro originated many times from separate seed.

15.2.3 Geographical range and dispersal of triploids

Triploids occur mostly in Asia, and few have been reported for the Pacific Islands (Yen and Wheeler 1968; Sakamoto et al. 1976; Kuruvilla and Singh 1981; Coates et al. 1988). Recent historical explanations for the occurrence of triploids in New Zealand and New Caledonia were suggested by Yen and Wheeler (1968) and are discussed in Chapter Fourteen. Recent introductions of taro from Asia to the Pacific have been widespread. McKnight and Obak (1960: 5–6) reported that a taro variety was introduced to Palau (Micronesia), directly from Japan, by Japanese in the present century, and that this variety was largely cultivated by non-Palauans at the time of writing (late 1950s). Whitney et al. (1939: 7) reported that Chinese immigrants commercialised taro production in Hawai'i on a large scale from the latter part of the nineteenth century. One variety (*Bun-long-woo*) from China and three from Japan (*Akado*, *Tsurunoko*, and *Miyako*) were described (Whitney et al. 1939: 9, 24). It is likely that triploids were included among these recent introductions to the Pacific.

As noted in Chapter Fourteen, because triploids are sterile, the wide geographical range of triploid taro within Asia must be the result of dispersal by humans, and dispersal

by humans was probably largely an agricultural phenomenon. Before discussing the general absence of triploid taro in the Pacific Islands, explanations for the origins and prevalence of triploids in Asia are considered.

Within Asia, triploid cultivars are common in temperate Japan (Sakamoto et al. 1976: 44; Kawahara 1978) at high altitudes in Nepal (Kawahara 1978) and in the northeastern hills of Meghalaya, India (Kuruville and Singh 1981). Kawahara (1978) suggested that diploid and triploid taro may differ in their physiological responses to high altitude or high latitude, and Kuruville and Singh (1981) suggested that triploids evolved in response to the climate of the Meghalaya hills. Because of their sterility, evolution by triploids would be restricted to somatic mutation within clonal lineages. Adaptation to high altitude or temperate (high latitude) climates may have required prior breeding and natural selection among wild diploid populations. Cultivated diploids are not completely absent from Nepal, the Meghalaya hills or temperate Japan. If wild diploids were also present in any of these areas, and did reproduce by sexual means, then triploids could have been created that were adapted to higher altitudes and temperate climates. Such triploids, even if very rare in their original occurrence, could have become common in many areas of similar climate in the hands of agriculturalists. Triploidy, in itself, may have conferred some advantage for cultivation at high altitudes or latitudes, and no particular advantage in tropical areas.

The evolutionary response to climate suggested by Kuruville and Singh (1981), noted above, can also be read as implying that triploids originated because of conditions in the Meghalaya hills. If climates in hill areas of northeastern India are marginal for sexual reproduction, then environmental stresses may have induced irregularities in gamete production and the subsequent production of triploids. Marginal conditions for sexual reproduction might exist in many areas. In Japan, it appears that taro does not reproduce sexually because of the low autumn temperatures (Hirai et al. 1989), but conditions may be marginal for sexual reproduction in the warmer Ryukyu Islands and in the hill areas of southern China. Triploids may be common in marginal areas not because of any particular advantage for cultivation, but because they are more likely to be created there.⁷⁾

15.2.4 Absence of triploids in the Pacific

Several explanations can be suggested for the apparent absence of triploid taro in the Pacific before the recent historical period: (1) no taro were introduced by humans, from Asia to the Pacific; (2) few triploids were introduced because few taro, overall, were introduced; (3) triploids were not introduced because human dispersal of taro from Asia occurred before triploids became common in Asia; (4) the source areas within Asia for introductions to the Pacific were areas that lacked triploids; (5) triploids were not created in the Pacific; and (6) triploids did arise in the Pacific in the wild, but did not enter into cultivations to become sufficiently common for detection in surveys of chromosome numbers.

Yen and Wheeler (1968: 265) argued that the common occurrence of both diploids and triploids in Asia, and the lack of triploids in the Pacific, might reflect early dispersal

of diploids from Asia to the Pacific, before triploids became common in Asia (see (3), above). The earlier dispersal of diploids from Asia into the Pacific was regarded as being associated with agriculture (Yen and Wheeler 1968: 263), and it was thus implied that cultivated triploids became common in Asia relatively recently. This is consistent with the argument (previous section, above) that the wide geographical range of triploids was the result of agricultural dispersal. Subsequently, Coates et al. (1988) suggested that diploid taro first arrived in the Pacific as part of the natural eastward extension of the Indo-Malaysian flora into Sahul (after the early Miocene). This implies that the initial Pacific appearance of diploid taro was prehuman, and thus preagricultural. The likely pre-agricultural and possibly prehuman introduction of taro into the Pacific was discussed in the first part of this chapter. If it is accepted that the triploid taro group has multiple origins, and that diploids are indigenous in both Asia and the Pacific, then other explanations can be given for the absence of triploids in the Pacific, in addition to the possibility that triploids were of recent origin in Asia. In view of these two considerations, it is necessary to examine the above arguments (1) to (6) more closely.

No taro were introduced

Taro may be indigenous to Australia and New Guinea, so it cannot be assumed that all cultivated diploids were introduced from Asia. It remains to be seen whether or not Pacific cultivars are more closely related to wild taro in New Guinea than wild taro in Asia.

Few taro, overall, were introduced

If few taro were introduced from Asia during prehistory, then the statistical chance of triploids not being included may have been significant, even if triploids were present in the source areas. The great phenotypic diversity of diploid cultivars in the Pacific does not exclude the possibility that few introductions were made. Even a very few early introductions could have generated many new, diverse varieties in the Pacific by breeding in feral populations and by crossbreeding with wild populations of pre-agricultural origin. The overall rate of introduction from Asia may have never been very great. If introductions from Asia were made only very recently, within the agricultural period of Pacific prehistory, then there might have been too little time for Asian diploids and triploids to spread in the Pacific. Most diploids cultivated in the Pacific Islands could have originated in New Guinea, either directly or through subsequent breeding in feral populations beyond New Guinea.

Dispersal from Asia occurred before triploids became common in Asia

This argument, by Yen and Wheeler (1968), is noted above.

If the occurrence of triploids is time dependent, and results from genetic aberrations independently of environment or genotype, then most triploids were probably created during the long period of natural evolution in Asia, before human utilisation of the species. The possible environmental induction of triploids was noted above. Here, consideration is given to two further possibilities: firstly, the creation of triploids might

have been dependent on the existence of particular diploid genotypes, and secondly, the generation of suitable diploid genotypes may have been promoted by human actions.

For many polyploid crop species, polyploidy appears to have been a consequence of hybridisation between different species (Simmonds 1979: 284). The genomes of two different diploid species can be represented as AA and BB. The hybrid genotype, AB, produced by two such species, may well be highly infertile if there is insufficient homology between the A and B genomes for proper pairing at meiosis. Often, instead of unbalanced haploid meiotic products, a very small but significant percentage of unreduced gametes (AB) may be produced (Briggs and Walters 1984: 181). Rare unreduced gametes would usually encounter normal haploid gametes (A or B) after self- or cross-pollination, resulting in triploid plants (ABB or AAB).

The rDNA analyses described in Chapter Thirteen indicated that *C. esculenta* is genotypically homogeneous, and may therefore represent one biological species. It nevertheless remains quite possible that the genomes of some taro varieties are sufficiently different from each other for there to be some degree of infertility, and irregularity in cell division, among the allo-diploid progeny of cross-matings. An acceleration in the dispersal of taro varieties may have started when humans first began to use taro, perhaps before agriculture developed and certainly afterwards. If the varieties carried by humans, within and beyond the natural geographical range of taro, were brought into contact with very different varieties, then the generation of allo-diploids and allo-triploids may also have accelerated.

This argument suggests that most triploid taro are allo-triploids, and this is consistent with the complex rDNA patterns noted for triploids in Chapter Fourteen (Figures 14.8 and 14.9). Although homozygous, non-allopolyploid plants can display complex rDNA patterns, as discussed in Chapter Fourteen, mixtures of different rDNA variants and complex rDNA patterns are, in general, likely to reflect allopolyploidy. Coates et al. (1988) present cytological evidence for the existence of auto-allopolyploid (heterozygous) and autopolyploid (homozygous) triploid lineages.

During the pre-agricultural and agricultural periods, the absolute numbers of sexually reproducing taro probably increased dramatically following human dispersal of wild and cultivated taro and the establishment of feral populations in the vicinity of cultivations. Even without genetic mixing effects, increased absolute numbers of wild taro may have increased the overall rate of triploid production. At the same time, presumably, agricultural traditions of variety selection, trial, and propagation became widespread, providing opportunities for sterile triploids to enter into cultivation and the dispersal routes of cultivars.

The processes suggested above are equally plausible for Asia and the Pacific. The particular genotypes required to produce triploids may have arisen only in Asia, or other factors may have been limiting for the occurrence of triploids in the Pacific. The suggestion of causal relationships between human actions (dispersal and propagation of taro) and triploidy provides, for the first time, an explanation for the possible recent production of triploids within the agricultural period. Most triploid varieties adopted by cultivators in Asia may have been derived partially or entirely from feral diploid

cultivars.

If triploids in Asia came into existence recently, sometime within the agricultural period, then diploid varieties of Pacific origin could have been transported to Asia at earlier times (probably also within the agricultural period), and could have been the progenitors of triploids in Asia. This could explain the occurrence of what appears to be the Queensland rDNA variant in Japanese taro (see Chapter Fourteen), if it did not originate early in the evolution of the species in Asia.

The source areas in Asia lacked triploid taro

All or most triploids could have been located outside the source areas for introductions to the Pacific. Although triploids have been found throughout tropical Asia, in the Ryukyu Islands, Taiwan, India, Philippines, Borneo, and Timor (Yen and Wheeler 1968; Sakamoto et al. 1976; Kuruvilla and Singh 1981), the reports suggest that triploids are abundant in areas of high altitude and high latitude and less abundant in other areas. If evidence is found for the promotion of triploid production in climates that are marginal for sexual reproduction, then this would support the suggestion that triploids were not evenly distributed in Asia in prehistory⁷⁾.

Triploids were not created in the Pacific

Triploids may not have been created in the Pacific because suitable diploid progenitors were absent. This suggestion is contradicted by the observation (Coates et al. 1988) that one lineage of triploid taro (I-13 cytotype) is possibly derived from the diploid cytotype I-1, recorded for two wild plants from Australia and two cultivars from Papua New Guinea. The I-13 cytotype was discovered in the New Zealand triploid variety GP (Yen, pers. comm. 1988), a variety which is acrid, produces little starch, is stoloniferous, and lacks anthocyanin pigmentation (Matthews 1984). Phenotypically, this triploid is rather similar to the wild diploid taro recorded for Australia and New Guinea, which is consistent with the suggestion of a Pacific origin. Nevertheless, it remains possible that the wild diploid progenitors of var. GP were located in Asia, an area for which wild taro remain poorly known.

Triploids originating in the Pacific have not been detected

If triploids produced in the wild (via sexual reproduction) lacked the qualities desired by cultivators, then they are not likely to be detected in general surveys of cultivated taro. In the wild, they are likely to be rare with very localised distributions. Few wild plants have been tested in surveys published to date, so it is not surprising that few wild triploids have been encountered.

Notes

- 1) Haberle (1995) reported various distinguishing characteristics of taro pollen, and then found taro pollen in lake sediments dating from 9,000 to 6,000 years BP approximately, at Lake Euramoo in northeastern Queensland (Haberle 2005). This period corresponded to a period of

arrival and expansion of many rainforest taxa in the lake vicinity.

- 2) The genus name is hereafter given as *Colocasiomyia*, following Sultana et al. (2006) and authors cited therein.
- 3) Hunt et al. (2013) have since reported the presence of *Colocasiomyia* in Queensland, based on identification of an empty pupal cocoon collected in 1987. Further study is needed to identify the species present and determine its host range in Australia.
- 4) This and further finds of *Tarophagus* in Australia were reported by Matthews (2003).
- 5) Comparison of the biochemical defences of wild and cultivated taro remains a very promising area of study for understanding the domestication history of taro (Matthews 2010). The heat stability of taro trypsin inhibitor during cooking has been studied (Bradbury et al. 1992). Also of special interest are the heat resistance of lectins in taro corms (Seo et al. 1989), the cyanide content of the leaves and stems of edible aroids (Bradbury et al. 1995), and the acidity associated with calcium oxalate raphides (Bradbury and Nixon 1998).
- 6) This route of polyploid formation was later confirmed experimentally by Otsuka et al. (1995) and Isshiki et al. (1995).
- 7) Zhang and Zhang (1990, 2000) studied the distribution and abundance of diploid and triploid taros in China, and found them to be more abundant at higher altitudes and higher latitudes. They attributed this to greater hardiness, and noted that the process of polyploidization must have been important for the (subsequent) spread of taro into new areas (under cultivation), namely: Yangtze River area, central and north China. They also noted the widespread occurrence of wild taros in southern China, and suggested that triploids may have arisen in south and central China during a warmer climate period in that region (between 4000 and 1000 BC).

Chapter Sixteen

Origins, Dispersal, and Domestication

In Chapter Fourteen, field surveys and ribosomal DNA analyses were discussed, and possible directions for future genotypic analysis suggested. In Chapter Fifteen, further sources of biological information were described, and possible approaches for investigating the origins and antiquity of diploid taro in Australia and New Guinea were summarised. Particular attention was also given to the origins of triploid taro. Here, in Chapter Sixteen, I conclude the thesis by taking a broad view of the origins, dispersal, and domestication of taro.

16.1 Taro as a Highly Dispersive, Colonising Species

In contrast to cultivated soybean, which, like taro, is recognised as one taxonomic species, taro has been shown to possess a range of ribosomal DNA variants. Cultivated taro therefore does not appear to have originated and spread from a single homogeneous wild population or race, as may have occurred with soybean. Extremely heterogeneous natural populations of wild taro might exist where the species originated, in mainland Asia. If not, then the variability of cultivated taro probably reflects some degree of prior differentiation among wild taro populations outside the area of species origin. It is unlikely that rDNA variation arose *only* within the agricultural period of prehistory. The available evidence, from all sources, suggests that wild taro in Australia and New Guinea may have arrived before agriculture began in New Guinea, but whether or not the species arrived very early, before human colonisation in the late Pleistocene, is not yet known.

With its capacities for both vegetative and sexual reproduction, each affording alternative means of survival and dispersal, taro appears to be a highly dispersive, colonising species. If taro was able to spread naturally from mainland Asia to Sahul, then its natural range in mainland Asia might also be very wide, perhaps from peninsular India to eastern China. Indigenous selection and domestication of taro could have occurred in New Guinea, and over a broad geographical range in Asia. Without denying social reasons for the absence of intensive agriculture (e.g., Chase 1989), the genotypic and phenotypic homogeneity of taro locally (see Chapter 14) may have acted against its domestication in Australia.

The following discussion of origins, dispersal, and domestication focuses on the starch-producing capacity of taro, a trait directly subjected to human selection during domestication, and the evidence from rDNA analysis for the differentiation of diploid populations in different geographical areas. Focus on a phenotypic character directly subject to selection by humans is required in order to explain the dispersal of taro by

humans. Although variation in rDNA may affect phenotypic variation in characters important to humans, rDNA itself has never been the immediate object of selection through human preference or intention. The phenotypic effects of rDNA variation, and intergenic spacer variation in particular, are currently under investigation (e.g., Cluster et al. 1987) but are beyond the scope of the present discussion. Ribosomal DNA has significance here simply as an indicator for the genetic differentiation or otherwise of wild taro, and as an indicator of sources for taro introduced to the Pacific islands, beyond the possible natural range of the species.

16.2 Natural Variation, Geographical Range, and Prerequisites for Cultivation

Members of *Colocasia* Section Tuberosae Engl. (*C. esculenta*, *C. fallax*, and *C. affinis*) may have evolved naturally from their most recent common ancestor within the region of northeastern India, southwestern China, northern Thailand, and Burma. *C. gigantea*, in Section Caulescentes Engl., may have originated south or east of the other species, since its extant distribution is mostly south and east of *C. fallax* and *C. affinis*. If the fruit and seed of *C. esculenta* were readily dispersed by birds and small mammals, then this species may have spread naturally through coastal regions of mainland and island Southeast Asia, as far east as Australia and New Guinea. Wild varieties and probably races evolved in partial geographic isolation from each other, and in diverse ecological circumstances. The distributions of different rDNA genotypes in the wild taro of Australia and New Guinea suggest such differentiation (Chapters 6 and 7). Natural differentiation would have created different conditions for domestication and other forms of plant-human interaction in different regions.

C. affinis, *C. fallax*, *C. gigantea*, *C. esculenta*, *C. esculenta* var. *fontanesii*, *C. sp.* and wild taro common in Australia and Papua New Guinea share the stoloniferous growth habit (Figures 10.1 to 10.6) and it is proposed here that this habit is a primitive condition for the genus. The stoloniferous wild taro varieties of New Guinea and northern Australia, with very little starch compared to modern cultivars, could be similar to the earliest natural forms of *C. esculenta*. The other *Colocasia* species noted above also produce very little starch.

Was starch production the only prerequisite for initial cultivation of taro by humans? Other traits, such as medicinal properties or edible leaves, may have enhanced the usefulness of taro, or may have been sufficient in their own right. For example, if plants were initially cultivated for their leaves, then small yields of starch from corms might have attracted attention as a secondary product, leading eventually to the selection of varieties with preferred starch qualities. Alternatively, wild taro could have been managed in the wild for multiple purposes, including the provision of starch, before cultivation began. Cultivation is defined here as the creation of an artificial environment specifically for the propagation of the desired plants. If the first selections from the wild became the sole basis for subsequent vegetative propagation in cultivations, then little new genotypic variation would have been available for selecting increased starchiness effectively,

whatever the initial quality of starch production by the selected wild varieties. Cycles of breeding (sexual reproduction) and selection would have been necessary for humans to promote starchiness effectively.

If early forms of agriculture resembled modern swiddening systems, then there were probably ample opportunities for cycles of breeding and selection. Swidden systems readily generate feral populations when gardens are not completely harvested before being left to fallow, because unrestrained breeding occurs in fallow areas. Actively cultivated gardens may have been major sources of pollen for nearby feral populations, and for any nearby natural wild populations, if suitable pollen vectors were present. The likely pollinating insects for taro in Papua New Guinea were discussed in Chapter Fifteen.

Occasional harvests and replanting of feral and other wild varieties, or protection of useful wild varieties when old and new garden areas were cleared, would have brought sexual progeny with new genotypes (the products of segregation and reassortment) into assemblages of vegetatively maintained cultivars. In this way, swiddening systems probably provided ideal circumstances for breeding in the history of vegetatively propagated crops such as taro. Varieties producing more starch could have originated within an agricultural context, even if the species was first cultivated for reasons other than starch production.

Explanations for the evolution of starchiness in nature lead to suggestions about where wild varieties with desirable starch qualities might have existed before humans began using taro. In the literature on the evolution of starchy root, tuber, and corm crops (each differing according to the anatomical region in which starch is deposited, but collectively known as root crops), starch storage has been explained as a common and natural evolutionary response by diverse taxa to either seasonally dry and/or seasonally cold climates.

In a discussion of South American root crops, Hawkes (1989: 482) suggests that tropical root crops originated not in the equatorial, Amazonian rainforests, where there is no strong selection for the development of underground organs, but in areas north and south of the equator, where there are well-marked dry seasons. Sauer (1952: 40, cited by Hawkes 1989: 482) states that underground starchy reserves help plants to survive the dry season and to regenerate quickly when rains return. Hotta (1983) suggests that root crops in eastern Asia developed where species hibernated naturally in response to either seasonal dry periods or seasonal cold periods. Starchy cultivated varieties of taro, from the tropical region of Southeast Asia and the Pacific, including the southern islands of Japan, are intolerant of cold and are morphologically distinct from cold-tolerant varieties of temperate eastern Asia (Hotta 1983). Hotta suggests that there are several separate genealogies of cultivated taro, originating among diverse starchy wild types within a natural distribution range limited to mainland Southeast Asia (Figure 16.1).

The significance of human dispersal of taro in the temporally unlimited pre-agricultural period remains completely unknown. We cannot yet assess, in terms of genetic variation and geographical distribution, the role of early humans in establishing suitable circumstances for domesticating taro. Under the hypothesis of domestication over

a broad geographical range, a restricted natural geographical range remains as strong a theoretical possibility as a wide natural geographical range. A wide geographical range could have been the result of dispersal by humans before agriculture began, and there may have been time subsequently for differentiation of the wild populations from which cultivated taro were derived. The following discussion focuses on the possibility of wide natural dispersal.

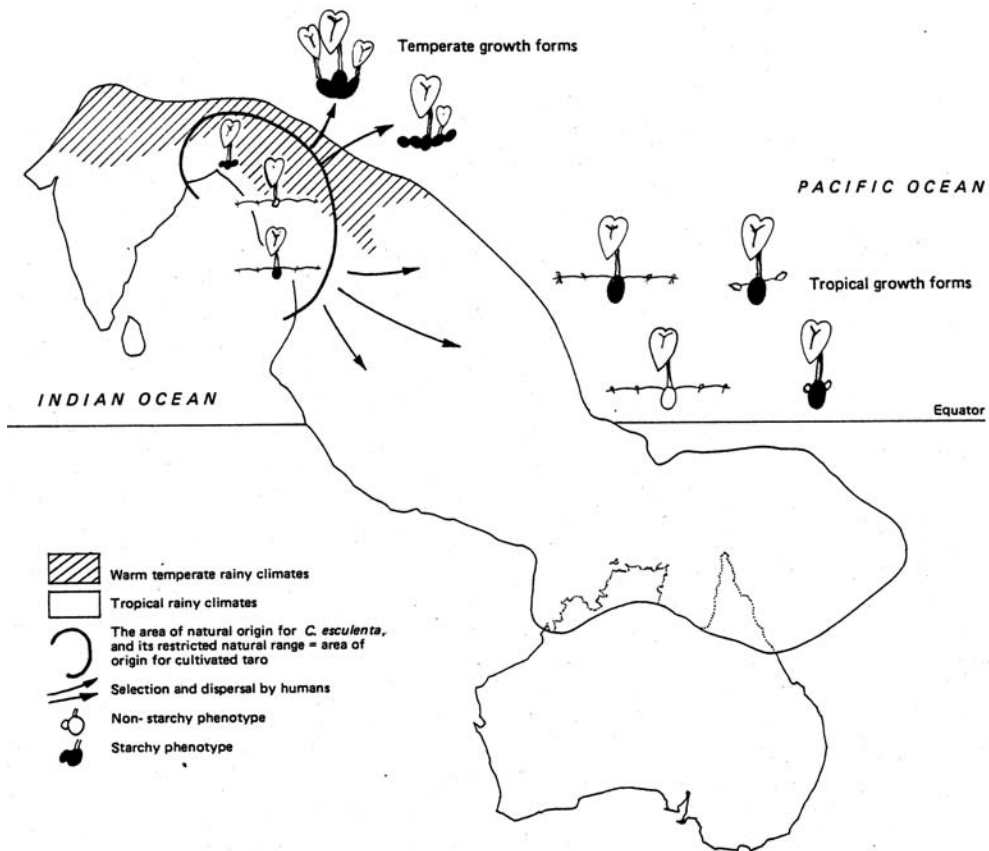


Figure 16.1 The possible restricted natural range of taro and a scheme depicting a single area of origin for cultivated taro. According to this scheme, the selection and dispersal of taro by humans began with starchy wild-types that evolved and dispersed naturally within a range restricted to mainland Southeast Asia. The theoretically possible natural range is also the likely area for the natural origin of the species. The large area outlined, encompassing India, northern Australia, and the area between, is the maximum theoretically possible range (see Figure 16.2).

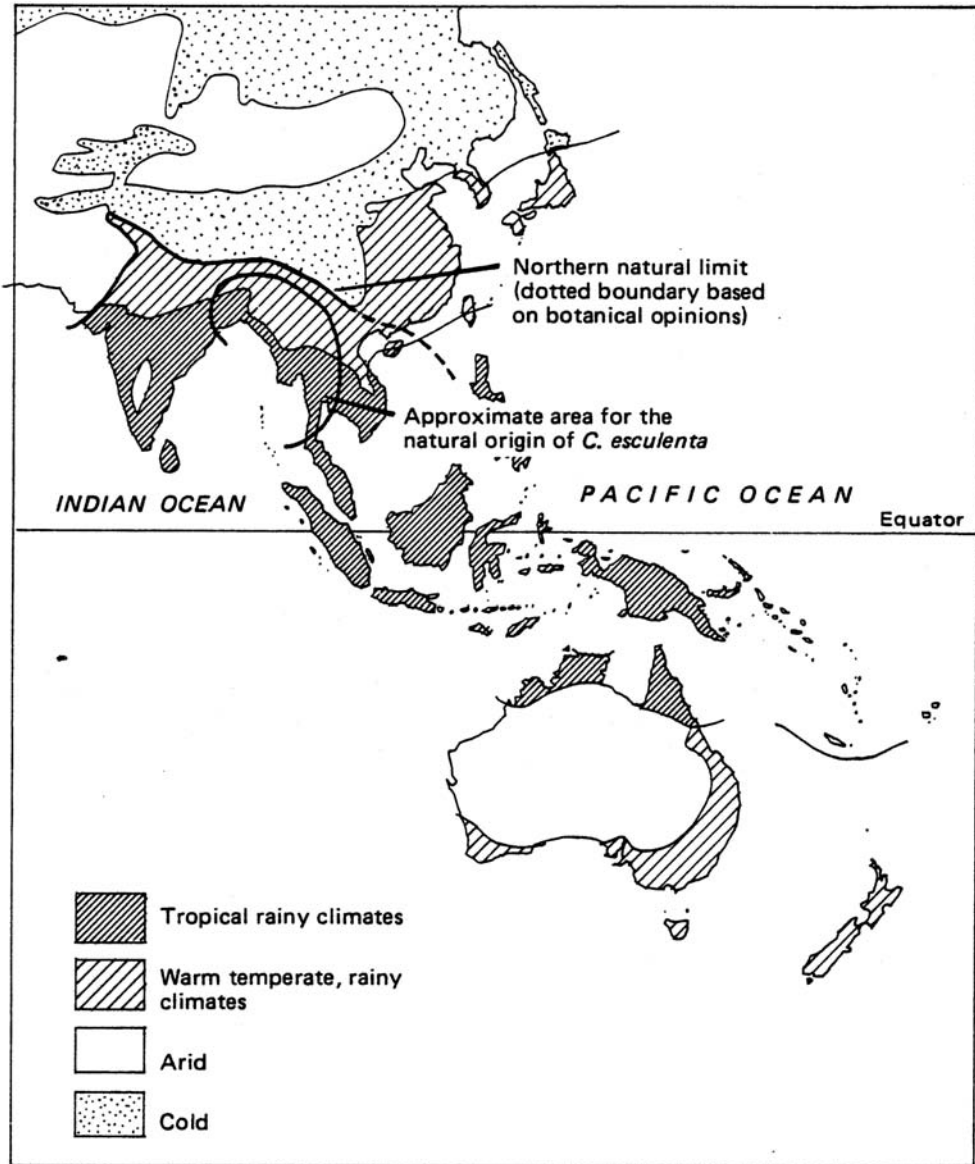


Figure 16.2 Climatic zones in Asia and the western Pacific. The origin of *C. esculenta* as a natural species is probably somewhere within the partly circled area. The maximum natural range considered possible, in theory, is limited by the Indian and Pacific oceans, by extreme cold and aridity in India and China, and by aridity in Australia. In eastern China, the natural range of taro may have reached its maximum extent within the warm temperate zone. Map adapted from Poynter and Atkinson (1984). Within the tropical rainy climate zone, seasonal shifts in surface winds produce the northern (summer) and southern (winter) monsoons, and bring heavy rainfall.

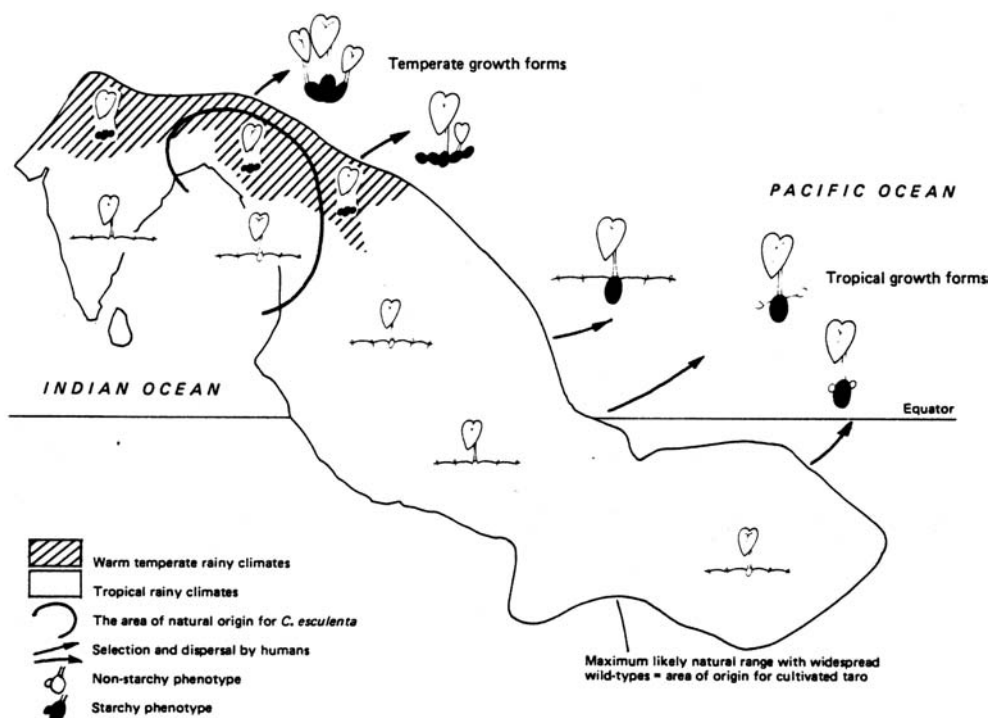


Figure 16.3 The maximum possible natural range for taro in Asia and the Pacific, and a scheme depicting the possible multiple geographical origins of cultivated taro. According to this scheme, the selection and dispersal of taro by humans began with non-starchy and starchy wild-types of wide natural occurrence, in the tropical and warm temperate zones respectively. The likely area for the natural origin of the species is also shown. The natural range outlined is based on the map shown in Figure 16.2.

16.3 The Maximum Possible Natural Geographical Range

The present geographical distribution of cultivated taro follows two major geographical and climatic axes (Figure 16.2). On a west to east axis, from India to Sahul, tropical rainy climates are found. These include perhumid climates in which wet tropical rainforests predominate, close to the equator, and monsoon climates with progressively longer seasonal dry periods, further north and south of the equator (Whitmore 1984: 55). In northern Australia, the summer monsoon rains follow a cooler dry period of about nine months.

On a south to north axis, from southern India and Southeast Asia to northern India and northern China, climates range from the tropical rainy types just described, through temperate rainy climates, to cold temperate rainy climates beyond the northern limit of cultivated taro.

Four major barriers define the maximum possible natural range of taro (Figure 16.3)

on the two geographical and climatic axes described above: (1) dry steppe and desert climates of northwestern India and central Australia; (2) the perpetually cold, high altitudes of the Himalayan mountains; (3) cold temperate climates of far western and northern China; and (4) the Indian and Pacific Oceans. Hay (1986: 3) notes that the diversity of the Pacific aroid flora (the botanical family of *Colocasia*) tails off eastwards very sharply at New Guinea, and that New Caledonia is devoid of endemic aroid genera, with only one, dubious, endemic species (*Rhaphidophora* sp.). The natural range of taro may extend as far as New Guinea, or somewhere farther east. The Malesian floristic region, in which many aroids occur, extends eastward as far as the Bismarck Archipelago, a limit that Whitmore (1984: 5) defines arbitrarily because no major forest-type boundary occurs between New Guinea and the Pacific islands. East of the Solomons, ocean gaps are almost certainly major barriers for natural dispersal by taro.

An absence of botanical records of taro in northern China (Li 1979), and the general belief that Japanese taro originated in southern China (see Chapter Fourteen), suggest that the northernmost natural limit for taro in China is within the temperate region (Figure 16.2). No wild taro, apart from those resulting from recent introduction, are known in the arid or temperate zones of Australia (see Chapter Ten, Figure 10.11), despite a history of extensive botanical exploration in Australia, and the possible southernmost natural extent of taro seems relatively well defined.

Vegetative growth habits and starch storage traits that might have evolved within the natural range, before human utilisation of taro, now become the subject of attention. The general relationships between latitude, longitude, and climate are assumed, for simplicity, to be broadly similar to those observed today, since the origins of the species in geological time and space are not known exactly.

16.4 Tropical Growth Forms

If the natural primitive form of *C. esculenta* possessed stolons and minimal starch reservoirs (as discussed above), then such a form could have arisen within the monsoonal region between India and Malaysia. In northern Australia, where a strongly seasonal dry/wet monsoonal climate prevails, the stoloniferous habit is undoubtedly important for survival. The stolons of wild taro can extend at least two metres, and probably more, with nodes from which new shoots grow and produce further stolons (personal observations in far northern Queensland). Stolons are water-seeking generative organs, and as such are an alternative to starch storage and dormancy for survival in monsoonal regions.

Among varieties of *C. esculenta*, stolons and side-corms are the major alternative forms of vegetative reproduction and dispersal, both forms of lateral shoot being readily dislodged and dispersed by water (a general field observation by the author). Stoloniferous wild plants also survive well in the wet tropical rainforests of northeastern Queensland and in Papua New Guinea, so it cannot be assumed that the stoloniferous habit evolved in response to monsoonal climate dry periods. However, if the stoloniferous habit is the primitive state for *C. esculenta*, then its retention may have lessened or

removed the need for starch storage as a response to seasonal aridity. Both rainforest and monsoonal forest regions could have accommodated the natural spread of taro, assuming that sufficient permanent water sources were available in monsoonal areas.

Stoloniferous wild taro synonymous with *C. esculenta* var. *aquatilis* (Hassk.) Kitamura (Hotta 1970) are known in Bengal, Malaysia, the Ryukyu Islands, and Java (Engler and Krause 1920; Hotta 1970), and it is proposed here that the wild stoloniferous taro of Australia and Papua New Guinea also belong to this varietal group. Haines (1924) presents the type description for *C. antiquorum* Schott var. *stolonifera* Haines, which he regarded as similar to the Javan var. *aquatilis* Hassk. The variety described by Haines was found wild and flowering along rivers near Ranchi and Palaman, Bihar Province, eastern India, in 1918 (H. H. Haines, Kew Herbarium sheets 4381, 4382), and is characterised as having green leaves and numerous long stolons, up to three metres in length. Mitra (1958) reports that *C. antiquorum* var. *nymphaeifolium* (Vent.) Engl. (syn. *C. esculenta* var. *aquatilis* [Hassk.] Kitamura in Hotta 1970) is wild throughout eastern India and Bengal, and it seems likely that var. *stolonifera* Haines, is an Indian form of var. *aquatilis* (Hassk.) Kitamura.

Although some occurrences of *C. esculenta* var. *aquatilis* may be primitive cultivars or represent naturalised (feral) lineages (Hotta 1970), var. *aquatilis* appears to be a widespread natural wild-type of the tropical region.

16.5 Temperate Growth Forms

If the non-starchy, stoloniferous habit is the primitive condition of *C. esculenta*, then starch deposition and side-corm formation are presumably derived (modern) traits, whether of natural origin or the outcome of domestication. At higher altitudes, growth is limited more by low temperatures and shorter day lengths than by water shortage, and stoloniferous varieties may have spread less successfully there than varieties with seasonally dormant starchy corms and side-corms. Winter dormancy improves survival in cold temperatures by corms and side-corms, whether in the field or as a stored harvest, and starch deposition provides shoots with reserves for renewed growth in spring. In mainland Asia, where *C. esculenta* is thought to have originated as a species, tropical rainy climates and warm temperate climates merge over short latitudinal and altitudinal distances (Figure 16.2). In this area, the differentiation and spread of different varieties under different climatic regimes could have begun early in the history of the species. The distribution of possibly natural wild taro does not extend to temperate southern Australia, and there is no reason to propose the differentiation of temperate adapted forms at this geographical extreme.

Hotta (1970) grouped all cultivars under the name *C. esculenta* var. *esculenta*. Within this variety diverse cultivar groups are differentiated according to chromosome number and morphology. *C. esculenta* var. *esculenta*, as described by Hotta (1970), is essentially a broad convenience category for most cultivated taro. Diverse cultivar groups were also described by Whitney et al. (1939) for Hawai'ian cultivars; Kitamura (1949), Hotta (1970), and Hirai et al. (1989), for Japanese cultivars; and Ghani (1984) for

Malaysian cultivars. The classifications embrace starchy phenotypes that could have originated in either temperate or tropical regions, as natural wild-types or as products of domestication. Starchy and temperate adapted natural wild-types have yet to be identified in the field, and may be difficult to find since human activities could have resulted, directly or indirectly, in the loss of most natural populations of Asian taro.¹⁾

16.6 The Multiple Origins of Cultivated Taro

It is proposed here that indigenous selection and domestication of taro occurred over a wide geographical range and involved genotypically and phenotypically diverse natural wild varieties. This proposition is illustrated in Figure 16.3 and discussed below.

16.6.1 Climatic and geographical extremes

At the temperate geographical extreme, starchy varieties evolved naturally in response to seasonal periods of low temperature and shorter day length. Subsequent selection and dispersal within traditional agricultural systems, which fostered genetic interactions between cultivated and wild populations, promoted fast summer growth, survival of winter storage, and improved starch production (quantity and quality).

At the tropical extreme, there is not yet any direct evidence for taro that starchy wild-types evolved in response to seasonal dry periods. Rather, there is a widespread stoloniferous wild-type, *C. esculenta* var. *aquatilis*, which in Australia and Papua New Guinea produces small acrid corms with very little starch. Where local wild populations of this variety expressed genotype-dependent variation in starch production, selection by humans in the wild and within cultivations could have transformed the relatively non-starchy wild-type into the cold-sensitive and starchy, stoloniferous, short-stoloned, and non-stoloniferous varieties now common in tropical areas (for example, the Mikashiki and Oyaimo cultivar groups described by Hotta 1983).

In the survey of rDNA variation, triploid cultivars from Japan and diploid wild varieties from Australia and Papua New Guinea represent opposing extremes in terms of geographical location, climate, and habitat. Contrasts established by these samples are discussed below.

16.6.2 Temperate Asia

Although many triploid taro varieties may have arisen through sexual processes in natural wild populations, the wide distribution of triploids in Asia largely reflects human agricultural activities (see discussion, Chapter Fifteen). The inherent sterility of triploids surely prevented them from having any major role in natural pre-agricultural evolution of the species. Among triploids, variations in rDNA (Chapter Fourteen), chromosome morphology (Coates et al. 1989), and phenotypes all point to the origins of triploids among diverse diploid varieties. The progenitors of triploids in temperate Japan and China were presumably temperate-adapted and starchy wild diploids, since genotypic change among triploid cultivars was limited to vegetative mutation. The agriculturally favoured qualities found among the diploid progenitors probably arose through a

combination of prior natural evolution and subsequent selection within agricultural systems. The starchy and temperate adapted natural wild-types predicted here (Figure 16.3) have yet to be identified in the field, and might be difficult to find since human activities could have resulted, directly or indirectly, in the loss of natural populations of Asian taro¹).

16.6.3 Tropical Pacific (Australia and New Guinea)

The absence of intensive taro cultivation in Australia is undoubtedly related to cultural factors, since contacts between the northern inhabitants and agricultural outsiders like the Macassans, if only within the past 400 years (MacKnight 1986), and the Torres Strait Islanders (Harris 1977; Barham and Harris 1983), for a certainly much longer time period, did not result in the transfer of agricultural techniques.

Despite the exploitation in northern Australia of many plant taxa used in agriculture in southeastern Asia, all Aboriginal groups routinely pursued hunter-gatherer modes of subsistence (Golson 1971b; Chase 1989: 51). Chase suggested that with the development of highly complex and deeply integrated religious beliefs and practices, societies such as those in Aboriginal Australia may have passed a critical threshold for receptivity to the agricultural practices of neighbours or visitors. In the Torres Strait, north of the islands of the Prince of Wales group, yams appear to have been the principle root crop, with sweet potato, taro, banana, and sugarcane also raised as staples (Harris 1977: 442). Taro is not recorded as a traditional crop for the islands closer to Cape York, where horticulture was less firmly established (Harris 1977: 442; Tucker pers. comm. 1987). Further southwards, in the Lockhart area of eastern Cape York, wild taro is regarded locally as native, and until recently was harvested as a staple food (Harris 1977: 433; R. Tucker pers. comm. 1987) (see Appendix 18).

From the above, it is clear that Australian wild taros were geographically isolated, and therefore genetically isolated, from agricultural populations of taro. Ribosomal DNA in Australian wild taro is homogeneous within sites and within regions, and is only known to vary between regions (Chapter Fourteen). Genotypic homogeneity on a local scale may have prevented effective selection by humans for improved starch production. Restricted dispersal of taro varieties within Australia, whether by natural means or by humans, and isolation from potential genetic sources outside Australia, may have preserved the genotypic integrity of wild taro populations that were unsuitable for domestication. Taro were possibly not domesticated in Australia for three reasons: cultural barriers to adoption, relative remoteness from potential sources, and the lack of suitable genotypes among the wild plants available locally within different regions of northern Australia.

Domestication is a synergistic process, in which human selectivity and environmental modification by humans (e.g., cultivation) are combined over time. This combination can lead to dramatic changes in plant productivity that could not arise from selection entirely in the wild, or simply by environmental modification without selective propagation from a range of genotypic variants. A detailed characterisation of what is a domesticated plant, the 'domestication syndrome' (Hanelt 1986), cannot be applied to all the cultivated taxa

commonly regarded as domesticated. Hanelt (1986) therefore defines the domestication syndrome as the crop-specific combination of characters which evolved in response to natural and artificial selection, under growing conditions essentially shaped by human activities. It is in this sense that cultivated starchy taro varieties are regarded here as domesticates.

If future genetic investigations define the genotypic basis for traits favoured during the domestication of taro outside Australia, it should be possible to determine whether or not the genotypic basis existed in Australia for similar domestication processes. If such a basis *did* exist, and wild populations do prove to be of sufficient antiquity to have allowed domestication, then purely cultural and social explanations for the lack of domestication could be advanced.

According to the general model proposed in Figure 16.3, taro was domesticated in New Guinea. Although the wild taro located in Morobe Province during the present study are phenotypically similar to the Australian wild taro, rDNA analysis proved them to be different genotypically. Other genotypic variants of stoloniferous wild taro probably occur in other, as yet unsurveyed, parts of New Guinea. If genotypic homogeneity partly explains why domestication did not occur in Australia, then genotypic heterogeneity may partly explain why domestication did occur in Papua New Guinea. Wild taro in parts of Papua New Guinea may possess greater local variability than has been observed in Australia. (cf. Hunt et al. 2013).

16.6.4 Bridging the temperate-tropical divide

The origin of the Queensland rDNA variant described in Chapter Fourteen is not known. It appears widespread among tropical cultivated and wild taro, from Southeast Asia to the eastern Pacific islands, and may be a distinguishing trait for taro indigenous to the tropical region (Chapter Fourteen). This proposition can be tested by future surveys of taro from temperate Asia (identification of the Queensland rDNA variant as a minor component is only tentative for triploid cultivars from temperate Japan, Chapter Fourteen). It remains to be seen whether or not any one rDNA variant is typical of temperate forms of taro.

Within Asia, between the temperate and tropical geographical extremes, genotypically mixed populations and varieties may have arisen during the natural and agricultural history of the species. To investigate effectively the proposed evolutionary division of *C. esculenta* into a temperate and a tropical group, and possible interactions between the two, it will be necessary to survey phylogenetically informative DNA sequences associated with different organelles (chloroplast, mitochondria, and nuclei) and different modes of genetic transmission.

16.7 Beyond the Natural Geographical Range

Beyond the northern limits of the natural range of taro, survival of the species depends on agriculture.²⁾ Most new cultivars in northern regions originated as introductions from areas where sexual reproduction allowed genetic interactions between cultivated and wild

populations, and within wild populations. Some new varieties undoubtedly arose by vegetative mutation within cultivation, both within and beyond the natural geographical range. The stability of rDNA variants in clonal lineages (New Zealand rDNA survey, Chapter Eleven; *C. esculenta* var. *fontanesii*, Chapter Fourteen) and the stability of rDNA in Queensland over a long history of vegetative and sexual reproduction (Chapter Fourteen) are consistent with the general view that new plant varieties arise more readily by sexual reassortment among existing varieties than by new mutation in either vegetative or gamete-producing cell lineages.

On the tropical axis of distribution, sexually reproducing feral populations were easily established within and beyond the natural geographical range of taro, where water was sufficient. It is probable that new varieties were generated in the wild throughout the tropical Pacific.

If cultivated taro accompanied the Austronesian speakers who moved from Southeast Asia into the Pacific, then breeding between Asian introductions and indigenous Pacific taro probably has occurred in the western Pacific, where close contacts were made between speakers of Austronesian and speakers of other languages. The human interactions involved are currently under investigation by anthropologists and linguists (Pawley and Green 1985; Blust 1988; Ross 1988), archaeologists (Allen 1984; Gosden et al. 1989), and human biologists (Hill and Serjeantson 1989). Sorting out the genetic history of taro, and the associated human history, will be complicated if breeding between introduced and indigenous taro varieties was common, if cultivars came from parts of Asia where temperate and tropical gene pools were mixed, and if the movement of taro from the western Pacific was bidirectional, westward into Asia and eastward into the Pacific. Nevertheless, when cultivated and wild taro in Asia are better known, it might be possible to distinguish introduced and indigenous genetic lineages in the western Pacific, and the derivations of varieties introduced to the far oceanic islands of the Pacific.

Some indirect inferences regarding taro on the Pacific islands can be made from the observations of taro in Aotearoa (New Zealand). In Aotearoa, the historically recent disappearance of tropical Pacific (Polynesian) diploid cultivars was accompanied by an equally recent proliferation of introduced, cold-tolerant triploid varieties (see discussion in Chapters Eight, Eleven and Fourteen and Matthews 1985). Ribosomal DNA analysis and historical records indicate that the cultivated triploid varieties RR and GR have affinities with cultivated taro in temperate Asia (probably China, Chapter Fourteen). The rapid loss of traditional diploid varieties in Aotearoa suggests that introductions from the tropical Pacific islands, during prehistory, were cold-sensitive and only survived in cultivation. Cold-tolerant, diploid varieties in Aotearoa would have survived in the wild, as cold-tolerant triploid varieties do today, because special care would not have been required to maintain them. Assuming that the (now absent) diploid taro varieties in Aotearoa were typical of tropical Pacific varieties, then it appears that temperate-adapted Asian varieties did not reach (or did not survive in) the Pacific islands, before taro first reached Aotearoa.

During colonisation of the Pacific, migrants of Asian descent (the Austronesian speakers) may have acquired tropical, cold-sensitive diploid taro from the New Guinea or

nearby islands, and/or from the tropical region of Southeast Asia. This is consistent with interpretation of the Queensland rDNA variant (Chapter Fourteen) as a monophyletic variant, distributed throughout tropical Asia and the Pacific, and possibly absent in temperate Asia.

Notes

- 1) In China, 'loss of most natural populations' now seems less likely given the genetic and morphological diversity of wild taros reported there (Zhu et al. 2000), though it is still not clear which wild populations have natural origins, and which are derived from naturalised (feral) cultivars.
- 2) In particular, survival depends on the ability of farmers to keep planting materials alive despite cold winter temperatures. This is achieved through a variety of storage methods, and by trade between warmer and cooler locations (Matthews 2002).

PART 4

NATURAL AND CULTURAL HISTORY

This volume concludes with a brief review of selected work on taro by the author and others since 1990, after the work reported in Part 3. Some general trends are considered first, then specific historical themes related to the natural and cultural history of taro.

Chapter Seventeen

General Trends in Taro Research

Historically, research on taro has been scattered, discontinuous, and dependent on the efforts of isolated individuals or small teams. There is no international centre for research on taro, despite its status as an ancient and globally distributed food plant (Rao et al. 2010). Although traded internationally as a food product, taro has not become a large-scale commodity crop like corn, potato, rice, soybean, or wheat. Over much of its range, local use of taro has continued since antiquity without direct interference or support from public authorities or private companies. Nevertheless, modern transport has made it easy for cultivars (and associated pests or diseases) to move quickly and far, through personal exchange, local trade, long-distance trade, and agricultural research activities.

At present, the continuing spread of Taro Leaf Blight (TLB) (*Phytophthora colocasiae*; Figure 17.1) (Singh et al. 2012) may be the biggest driver of change in taro production, the spread of new cultivars between different regions of the world, and the composition of local cultivar assemblages. For historical research this is problematic, as the changes are happening far more quickly than our ability to record the characteristics and historical significance of many cultivars. Historical research is fundamental to understanding the practical value and potential of a cultivar, its dispersal history and present distribution, its conservation status (endangered or not), and its cultural value. Ideally, farmers and users will always have access to old and new cultivars, to allow adaptation to changing social and environmental conditions, and to enjoy continuity in the use of culturally significant varieties. Even when old cultivars can no longer be grown in one area, because of their disease susceptibility or for other reasons, they may be suitable for use in other areas, or may have important qualities for plant breeding.

Given the limited funds available for taro, globally, most agricultural research on the crop has been focused on local and immediate needs such as the collection, conservation, identification, and description of cultivars (cf. IPGRI 1999), testing for agronomic and food qualities, testing for resistance to diseases and pests, selecting improved cultivars for diverse conditions, and minimising the number of living plants that need to be kept in collections while maximising the diversity preserved (Quero-Garcia et al. 2004; Mace et al. 2010; Taylor et al. 2010). Living collections of taro are inherently labour-intensive and expensive to maintain, and *in vitro* conservation methods such as tissue culture require continuous support for the required laboratory facilities and technical staff. Ultimately, the conservation of genetic diversity in taro will depend on people wanting to use the plant. For this, more attention needs to be given to the maintenance, development and use of culinary knowledge concerning taro (Matthews 2004b). In recent years, researchers involved with taro have turned towards a more decentralised model of



Figure 17.1 Early (above left) and advanced (above right) symptoms of Taro Leaf Blight (TLB) caused by *Phytophthora colocasiae*, on taro cultivars being tested at the National Institute for Agricultural Research (NARI), Bubia, Papua New Guinea. Below: shade house built at Bubia to grow taro seedlings produced in experimental crosses (2010, with J. Waki).

conservation, breeding, and cultivar dissemination. This is aimed at — and requires — participation by local universities, agricultural research organisations, farmers, and consumers (Lebot et al. 2005; Singh et al. 2010; INEA 2011).

There has been no general effort to study the food uses of taro (Matthews 2004b, 2010), the diversity of production systems for taro (despite some early academic interest — see Spriggs 2012), or the diversity of social and cultural values associated with the crop (e.g., Caillon 2012, and others in the same volume). There has also been no general effort to study wild populations of taro, other wild species in the same genus, and the relationships between these wild relatives and cultivated taro. My own



Figure 17.2 Corms of different elite cultivars being prepared for a taste panel at the Lowlands Agricultural Experiment Station (LAES), Kerevat, Papua New Guinea. Qualities such as acidity, taste, aroma, and texture will be tested by several different people who are regular consumers of taro, and the results pooled to assess the quality of the cultivars for commercial production and general consumption (2010, with R. Moxon).

ethnobotanical surveys have been very limited in geographical scope, and have been focused on wild taro populations (as reported in this volume; Matthews, Takei and Kawahara 1992; Matthews and Naing 2005; Matthews 2006; Matthews et al. 2012). Such work is difficult to organise from outside each country where taro is grown and used, and the number of countries where such work could be carried out is huge, since the crop is global in distribution. My hope is that the present volume can serve as a starting point (despite many flaws, or perhaps because of them) for students and researchers in many different countries. Much new work can be done now through systematic use of information sources, translation tools, and social networks supported by the Internet, but even this will be a large undertaking, and the quality of information that can be obtained in this manner is highly variable.

Research on the natural and cultural history of taro can show us how the crop has traditionally been maintained *in situ*, reveal threats to populations of wild taro and wild relatives, and help us develop conservation strategies where these are most needed (cf. Hunter and Heywood 2011). Studies of the wild relatives are fundamental to understanding the domestication process, the genetic and geographical origins of the crop, and relationships with organisms that appear as pests and diseases in cultivated taro. It is likely that traits present in wild taro populations and in close wild relatives have been largely ignored ever since human attention became focussed — thousands of years ago — on the qualities of selected forms present in gardens and around settlements. By looking at wild populations and relatives, we may discover (or rediscover) useful qualities that cannot be imagined until they are seen — or tasted. The corms of wild taros in most countries are considered inedible, or poor for eating, unless they are known cultivars planted in wild locations (as reported here in Chapter Seven). If known or new techniques can be used to render inedible wild taros edible, then unexpected but favourable qualities of taste, texture, nutritional content, or processing potential might be revealed. In cultivar trials and breeding programmes, it is usually the expected and familiar qualities that are tested (Figure 17.2).

Despite the obvious gaps in research, important historical insights have been gained through the efforts of many researchers and organisations since the late 1980s. Bioversity International (formerly the International Plant Genetic Resources Research Institute) has played a leading role in supporting conferences and the publication of research on taro (IPGRI 1999; Zhu et al. 2000; Guarino et al. 2004; Rao et al. 2010), and has encouraged ethnobotanical research on crops generally. This reflects a growing recognition that biodiversity, food security, and cultural diversity are interdependent (Pollock 2002; Maffi 2004; Nabhan 2009; Maffi and Woodley 2010). Previously, I noted that ethnobotany had the status of an orphan science (Matthews 1996), but this science (together with ethnobiology) has gained increasing recognition in recent years (Stepp et al. 2002; Ellen 2006; Fuller 2013). For those of us who identify with ethnobotany or ethnobiology, our academic homes are still mostly perched on the edges of other disciplines. Fortunately, common ground is not difficult to find, and the need to negotiate with other disciplines is probably a good thing. Ethnobotany is predominantly a field science, it is integrative in its practical and theoretical aspects, and its practitioners should be out in the world,

literally and metaphorically.

In the next chapter, I introduce some of the research that has been carried out since 1990, following the work reported in Part 3 of this volume.

Chapter Eighteen

Historical Themes

18.1 Cultivar Introductions and Food Preferences

In Part 2 of this volume I described three triploid varieties of taro that were and still are common in Māori communities of northern New Zealand. In Part 3, the possibility that two of these varieties (var. RR and var. GR) were historical introductions from China gained support in ribosomal DNA comparisons with the cool-adapted (temperate) cultivars of Japan, where many triploid cultivars are likely to have been introduced from China (over centuries or longer time periods). Ribosomal DNA analysis later proved very useful for distinguishing different cultivar groups in Japan (Matthews, Matsushita et al. 1992). Closely related cultivars within a cultivar group may have been introduced from outside Japan, but new cultivars in Japan are also known to have arisen through local mutation and selection. Ribosomal DNA patterns were constant within each of the main cultivar groups in Japan and were later surveyed in Japan, Taiwan, China, and northern Vietnam (Matsuda and Nawata 2002; Matsuda 2002). The triploid cultivar *Eguimo* is very similar (but not identical) with var. RR in phenotype and genotype (see Table 14.8, Figure 5.2), and cultivars with the same ribosomal DNA pattern as *Eguimo* have been found in northern and southern China and in northern Vietnam (Matsuda 2002).

The cultivation of taro has been a continuous tradition in New Zealand since long before the arrival of European and Chinese settlers, until the present. New cultivars continue to arrive, perhaps most often as undocumented introductions that follow modern immigration and food importation from the Pacific Islands (cf. Pollock 1992), Southeast Asia, and elsewhere. Plants have been grown from fresh corms imported from the Pacific Islands for markets in Auckland and elsewhere. Such introductions are mainly grown in home gardens, but some have also been adopted by botanical gardens and as ornamental plants. In New Zealand, a Cypriot immigrant family introduced the same cultivar of taro that I had previously seen growing in Cyprus, where taro is called *kolokasi* in the Greek language (Matthews 2006). I have also met Cypriot farmers in Australia who grow taro introduced from Cyprus; they sell the corms in Sydney where fresh taro from Queensland, Northern Territory, and the Pacific Islands can also be found. In 2009, I found *C. gigantea* (*bac hà* in Vietnamese; *hasu-imo* in Japanese, see Part 3, this volume) growing in Auckland, following its introduction by a member of the Vietnamese community (Figure 18.1). This may be the first record of *C. gigantea* in New Zealand. I have also seen *C. gigantea* flourishing in a suburban home garden in Sydney, Australia (c. 1994), and in 1997 found it growing in a community garden in Honolulu, Hawai'i (Matthews 1998), where Vietnamese immigrants often grow and use the plant (Nguyen



Above: Blades emerging in a small kitchen garden, alongside spring onion and other herbs used for making soup, North Shore, Auckland (2009). *Below:* Petioles peeled, cut, and cooked in soup (see central, long sections in mix), with wax gourd and other vegetables, as restaurant meal, Hanoi (2009). See also Figure 10.3.



Figure 18.1 *C. gigantea* (Bl.) Hook. f. in New Zealand and Vietnam.

2005). The petioles (leaf stems) can be cooked in soup after peeling, and it may eventually become a useful vegetable in New Zealand.

In 1991, M. Morishita of the Osaka Agriculture and Forestry Research Center kindly provided me with virus-free meristem tip cultures of two Japanese cultivars of taro, *C. esculenta*, which I then carried to Auckland for propagation and dissemination to interested gardeners and researchers (see Appendix 23). My aim was to introduce cultivars already adapted to the cool, temperate climate of New Zealand. Later, I sent further cultivars to J. Scheffer at the New Zealand Institute for Crop and Food Research, Pukekohe. The Institute also obtained plants directly from commercial seed companies in Japan. The new introductions were all tested in Auckland, and better performing cultivars



Figure 18.2 Production and use of taro leaves as a vegetable. *Above:* Large-scale cultivation of taro specifically for leaf production in southern Luzon, Philippines (2012, with M. Medecilo). *Below:* Leaves of a Japanese taro cultivar grown in South Auckland, and packaged for distribution throughout New Zealand. The leaves are kept fresh by cool storage and open wrapping in plastic (2011, courtesy New Zealand Kahoa Tauleva Trust).

were sent to further locations for trials (Scheffer et al. 1999; Bussell et al. 2004). Unexpectedly, Japanese cultivars have become a source of fresh leaves that are now grown in South Auckland (Figure 18.2) (Bussell and Triggs 2010), primarily for Pacific Islander communities that are unable to import fresh leaves from distant homelands. Coconut milk, an essential ingredient for Pacific Island cooking of taro leaves (as in the Philippines; see Matthews et al. 2012), is easily obtained as an imported, canned product. The common use of taro leaves with coconut milk in the Philippines and Pacific Islands may reflect a shared, ancestral cuisine, or independent discovery and appreciation of the taste and nutritional value of this combination.

In Japan, the leaf blades of taro are rarely recognised as a food. This can be stated with confidence as just a few local examples of such use were reported in a nation-wide survey of traditional foods, a survey that described in detail hundreds of recipes using corms or petioles (Rural Culture Association 1997). In Cyprus and Egypt, no part of the leaf is used, and in Cyprus the slimy mucilage produced by corms is strongly disliked. The sliminess is reduced by various preparation methods, before cooking, and by the addition of lemon juice during the cooking process (Matthews 2004b, 2006, 2010).

Culinary practices tend to follow long-established food preferences, and are associated with different vernacular names for taro, in many different languages. In theory, the full food potential of taro may be most easily developed in countries like Australia, New Zealand, and the USA, where diverse communities can share information and experiment with a range of imported and locally-grown cultivars. This will require cross-cultural dissemination of crop information, and careful translation of the vernacular names and recipes used by speakers of different languages.

The label on one bag of taro leaves sold in Christchurch, New Zealand (c. 2008) gave the following warning to new explorers, with good reason, but with no practical guidance (what is 'proper cooking'?):

'Raw taro leaves to be properly cooked before consumption. Should never be eaten raw.'

For the uninitiated, avoiding taro is usually the first preference, unless curiosity or hunger overwhelm caution.

18.2 Archaeology and Taro

18.2.1 Ancient starch

In the late 1980s, Tom Loy (then at the Department of Prehistory, ANU) began looking at starch residues on stone tools from Kilu Cave, Solomon Islands (Loy et al 1992; Loy 1994). Modern plant reference samples for that study were provided by the ANU taro collection, and led to the tentative identification of starch and calcium oxalate raphides from taro, from wild or cultivated sources (no differentiation could be made). Since 1992, with varying degrees of confidence, taro starch has been reported in archaeological contexts in Papua New Guinea (Crowther 2005; Fullagar et al. 2006), Pitcairn Island (Horrocks and Weisler 2006), Fiji (Horrocks and Nunn 2007), New Caledonia (Horrocks

et al. 2008), New Zealand (Horrocks and Barber 2005), China (Lu 2006), and elsewhere. The identification of ancient taro starch granules is especially difficult, due to their small size, simple shape, and similarity to the immature or smaller starch granules of other plant species. The most reliable identifications may be those made when taro-like starch granules are found *en masse*, in groups or clusters, along with taro-like raphides.

Ancient starch, with or without identification, has been reported in a huge variety of cultural, temporal, and physical contexts (Torrence and Barton 2006; Shibutani 2009; Henry et al. 2011; Haslam et al. 2011), but the archaeological work has not been supported by detailed biochemical studies of ancient starch, detailed taxonomic studies of modern starch, or the use of advanced techniques in histology and microscopy. Collins and Copeland (2011) note the need for more research on starch taxonomy and diagenesis, and question previous identifications of ‘cooked’ starch in archaeological contexts. The recent archaeological discoveries of ancient starch in very diverse geomorphological contexts offers biology and ecology a new and unexpected direction for investigating the fate of energy and carbon captured by photosynthesis and stored in starch. Ancient starch is likely to be present in many natural sediments, possibly at such low densities that it remains unavailable to micro-organisms (Barton and Matthews 2006). Optimising and calibrating methods for the extraction of starch from sediments could lead to new ways of understanding energy flow in natural and agricultural ecosystems, a fundamental issue for soil science, ecology, and the modeling of global carbon cycles.

It is also conceivable that starch derived from agricultural sources (and milling sites in particular) has washed out into shallow estuaries and near-shore deposits formed by the outwash from river deltas. In such near-shore sediments, deposits of ancient starch could provide a widely-dispersed signature for the arrival of agriculture (or milling techniques) in large river catchments.

18.2.2 Carbonised residues, macro-remains and pollen

As part of a wider effort to develop archaeobotanical techniques, and to make use of the micro-residues that are often abundant in archaeological contexts, Jon Hather pioneered methods for characterising the starchy tissues of various root crops, including taro (Hather 1991). This approach has led to identification or tentative identification of taro starch in Sulawesi, Indonesia (Paz 2005) and Timor-Leste (Oliviera 2012). Under very dry conditions, taro tissues can also be preserved, though few instances of this are known. At Quseir al-Qadim, Egypt, several dry fragments of taro corm were found, and two were radiocarbon dated to AD 1050–1170 (van der Veen 2011). Taro pollen were first described in detail by Haberle (1995), who then found taro pollen in lake sediments dated to the early Holocene in northeastern Queensland (Haberle 2005). This is the area where wild taro now is most abundant in Australia (Figure 14.3). The taro pollen first appears in the sequence as other pollen records show the region becoming warmer and wetter. When more is known about the natural range, ecology, and diversity of wild taro populations in Southeast Asia and the Pacific, archaeologists and botanists might like to revisit the various techniques of archaeobotany and palaeobotany in order to learn whether or not wild and cultivated lineages of taro can be distinguished through



Figure 18.3 Low-level production of taro using simple methods of protection, in naturally wet habitats. *Above:* wild taro (a wild-type?) protected with bamboo fences, without cultivation, on a muddy riverbank next to village (Ba Be, northern Vietnam; 2012, with D. V. Nguyen). *Below:* taro planted inside enclosures made by excavating the bank at left, and rearranging loose boulders from the stream bed; lacking containment, the soil here is minimal (Mount Mayon, central Philippines; 2013, with M. Medecilo).

observation of intact tissues (macro-remains), starch, pollen, and seeds.

18.2.3 Structures associated with taro production

Much of the interest by archaeologists in taro arises from the fact that modern taro production is often associated with the construction of drainage systems (to remove water) or irrigation systems (to supply water). Remnants of larger systems are relatively easy to find, archaeologically, or may remain obvious in the landscape long after their abandonment (Barber 1989; Bayliss-Smith and Golson 1992; Bayliss-Smith 1996; Denham et al. 2003; Denham and Barton 2006; Spriggs 2012; numerous contributors in Spriggs et al. 2012). Ethnographically, there are also many situations where natural slopes, or natural stream or riverbanks, are used to plant and grow taro on a small scale, with or without modification of ground surfaces (cultivation, stone arrangements, or larger earthworks). Even if low-level production (cf. Smith 2001) was common in the past, in a particular area, it might leave few archaeological traces. For taro, low-level and dispersed production is more likely to have allowed cycles of breeding and selection to occur (through relaxed control of the plant life cycle), and is more likely to have provided suitable contexts for domestication, initially and in later periods, and assuming some degree of selection pressure and isolation from wild-type populations.

At present, it is not known when, where, or how a tropical wild-type taro was transformed into a high-yielding starchy crop. A wild-type plant with naturally favourable qualities as a leaf, shoot, or starch source, for food or fodder, could have become widespread as a useful plant, in low-level production systems, before being domesticated anywhere within the wider range thus created. Eventual transformation through selection may have been a prerequisite or primary motivation for investment in the construction of larger scale production systems. Wild-type taro is likely to have reached Australia and New Guinea long before human arrival through natural dispersal (cf. Denham et al. 2009; Hunt et al. 2013). Its presence in New Guinea has been considered consistent with suggestions that taro was domesticated at an early date in New Guinea (see Part 3 and Matthews 1991), but this wild-type did not necessarily have any role in agriculture and domestication of the crop (Matthews and Terauchi 1994: 257). Genetic relationships with cultivated and domesticated forms of taro, and with wild taros in Southeast Asia, are currently under investigation (Ahmed et al. 2013).

Depending on intended uses, as leaf vegetable or as starch source, taro may also be managed with or without the addition or enrichment of soil in a production system. On a riverbank at Ba Be, in northern Vietnam, patches of taro that are considered locally to be wild and self-propagating are encouraged to grow by placing light bamboo fences around them (Figure 18.3). The fences help keep the plants in place when the river rises during the wet season, and the plants are used as a source of leaves for food and pig fodder. In a stream bed on Mt Mayon, Philippines, taro was planted in simple enclosures of loose boulders which cannot hold a deep soil, suggesting that the plants were grown for leaves and/or stolons, not corms (Figure 18.3).

Archaeologically, evidence for low-level production systems like those seen at Ba Be and Mount Mayon might be preserved by changes in a river course. After excavation

and discovery many centuries later, it would be difficult to distinguish protection of self-propagating wild plants, planting without cultivation, or planting and cultivation, if evidence for enclosures and plants was found. Evidence for stone arrangements or fences might easily lead to the assumption that the ground enclosed was cultivated. Use of the plants as leaf vegetable, and not as starch source, would also be difficult to distinguish. Archaeological discovery of seeds in the mud might indicate that neither the leaves (with immature inflorescences enclosed) nor corms were harvested, leaving open the possibility that stolons were the main target for harvest (Such use was observed by the author in a northern Luzon garden, in 2012). Alternatively, the plants might produce fruit and seeds soon after abandonment of a production system, before being covered with sediments.

Flowering and seed production by taro, in wild or cultivated environments, is highly dependent on the intended uses and harvesting methods. When allowed to flower, a single taro plant can produce thousands of seeds, and a large proportion of these may fall together with fruit in the vicinity of parent plants. The seeds do not float, and may be deposited in the near vicinity, even when there is some water flow on ground surfaces or in ditches. While surveying wild taro populations in Australia, Papua New Guinea, and Southeast Asia I have seen taro flowering and fruiting in many kinds of modified or loosely managed environments (Figure 9.3; Matthews and Naing 2005; Matthews et al. 2012; Hunt et al. 2013).

In recent decades, there has been some progress on the study of past and present taro production systems in the Pacific Islands (e.g. Hollyer et al. 1997; Spriggs et al. 2012), but relatively little work has been done in most regions of Asia or Africa. In Maputaland, South Africa, mixed cultivation of banana and taro in modified swamps (Grobler et al. 2004) may be of special interest for attempts to follow the movements of Austronesian-speaking peoples and their plants into Africa. In Cyprus and Egypt (Matthews 2006), I have observed taro production that is based on old Mediterranean or West Asian traditions of water management, though modern water shortages in the Mediterranean and West Asia will make it increasingly difficult to continue traditional methods of taro production in those regions. In Cyprus, taro now is mainly irrigated with water raised from underground sources, using mechanical pumps and deep pipe wells, rather than animal power and shallow hand-dug wells. In 1996, I learned from elderly informants that taro was also irrigated using channels from adjacent perennial rivers, earlier in the 20th century, before the rivers were dammed and the water diverted to distant areas for agricultural and urban uses. Archaeologists have long been interested in water management in the Mediterranean and West Asia, but mainly in relation to large-scale and extensive production of cereal crops and not the small-scale but intensive production of taro and other non-cereal crops.

Following fieldwork in Cyprus and northern Japan, I reviewed the use of storage systems to preserve taro corms as food and as planting material (Matthews 2002). These two uses can be associated with very different storage methods, since storage for consumption does not always require living shoots. When taro corms are stored for planting, in cooler regions, protection from cold is provided by the construction of various kinds of pit or covered mound. Structures designed specifically for storing taro



Figure 18.4 Taro (Greek: *kolokasi*) harvest in progress at Agios Georgos, Paphos District, Cyprus. The settlement is named after St George, the patron saint of agriculture. Irrigation water is supplied by a permanent spring nearby. After drying, the leaves will be cut away from the corms now on the ground. Many of the standing plants display inflorescences that cannot develop further under winter conditions. In antiquity, the small port below the present settlement was used for transshipment of grain from Egypt to Italy; Egypt today is a large-scale producer of taro (Matthews 2006) (October 1996, with P. Croft).

may have been preserved archaeologically, but have not been reported. This aspect of taro production has received little or no attention by archaeologists working in the temperate regions of Eurasia, Africa, and New Zealand. In Japan, it is likely that many ancient pits identified in generic terms as ‘storage pits’ were in fact pits located close to hearths for warmth and designed to keep taro corms alive during winter, for planting in spring. In contrast, green vegetables stored for consumption can be kept in cold storage pits, away from hearths. Specialised pits and other structures used to store taro planting materials may be widely distributed in the northern temperate zone of Asia, and in higher altitude farming areas in Himalaya.

18.3 Mapping and Describing Wild Taro Populations

Since 1990, and following the discovery of wild taro populations in northern Australia and Papua New Guinea (Part 3, this volume), my main goal has been to map the distribution of wild taro populations in Asia and the Pacific and to learn as much as possible about their ethnobotany, ecology, and genetic diversity. This work began in southern Japan (Matthews Takei and Kawahara 1992), then continued in Indonesia

(fieldwork 1992 and 1996), Australia (fieldwork 1994), Myanmar (Matthews and Naing 2005), Taiwan, the Philippines (Matthews, Takei and Kawahara 2012), and Vietnam (fieldwork 2011, 2012). Utilisation of wild taro populations is remarkably widespread, the main uses being as a green vegetable (young leaf blades, cooked) for human consumption, and as a green fodder (entire upper plant, cooked) for domestic pigs. Wild pigs have a natural liking for the young shoots and leaves of cultivated taro, in the raw state, and farmers often need to protect taro gardens from wild pigs.

Our recent study of chloroplast DNA sequences in taro (*C. esculenta*) indicates considerable diversity within the species (Ahmed et al. 2013). Different wild populations may belong to quite different genetic lineages and have different palatability for humans and animals. Deliberate dispersal of relatively palatable forms of wild taro as a food and fodder plant is likely to have occurred over long periods of time. Relating ethnobotanical data to the new understanding of genetic diversity in taro is a major challenge that lies ahead, as the exploration, description, and genetic analysis of wild taro populations continues. In few situations is it easy, on first sight, to recognise a wild population as part of a wider natural distribution of wild-types. Based on early experiences in Australia, Papua New Guinea, and Indonesia, a short field guide for describing wild taro populations was prepared (Matthews 1997, and Appendix 22). In Taiwan, *C. formosana* Hayata is a wild species that appears very closely related to *C. esculenta*. It is regarded by local botanists as a natural part of the flora. The ethnobotany, ecology, and genetic diversity of this species have not been studied. My impression also is that *C. formosana* is a part of the natural island flora, though human modification of the island landscape, vegetation, and fauna are likely to have had secondary effects on the distribution and abundance of this plant (Figure 18.5).

In the 1980s, many examples of wild and cultivated taro were assembled in a living collection maintained in Canberra, but this could not be kept for long after the PhD research project concluded in 1990. A small number of plants were kept for a short time for use in a pilot study of cyanogenic glucosides in wild and cultivated taro and in *Alocasia* spp. (Bradbury et al. 1995). In late 1989, with FAO support, part of the collection was sent to National University of Malaysia at Bangi, Selangor, but the plants do not appear to have been kept there. Since 1990, samples from a taro DNA archive established in Canberra have been kept by the present author in Japan. The archive now also includes dry leaf samples obtained during fieldwork in Japan and Southeast Asia and stored with silica gel. Many of these DNA and leaf samples have been studied by Ahmed et al. (2013), and some have also been compared with African taro samples by Grimaldi (2013), in collaboration with the SeaLinks Project of the University of Oxford, UK.

Most of the stored DNA samples have become degraded as a result of changes in location, and failures in refrigeration, over many years. Fortunately, modern techniques of DNA analysis allow even severely degraded DNA to be analysed. Samples of wild taro growing at a single location at Hope Vale, in northern Queensland (see Chapter Fifteen) were chosen from the archive and analysed for genetic evidence of breeding. The variability of simple sequence repeats (SSRs, or microsatellite loci) provided the first genetic confirmation of breeding in a wild taro population (Hunt et al. 2013). Breeding



Figure 18.5 *C. formosana* Hayata on roadbank (at right) in Wulai district, northern Taiwan (2013, with K. C. Tsai).

by taro in Papua New Guinea was previously confirmed by observation of insect pollinators (Figure 15.1), fruiting and seed production (Figure 9.3), and a report of seedlings (Price et al. 2008) (see also Ivancic and Lebot 2000). Taro seedlings in northern Australia have not yet been reported, but are expected; the main period of flowering and fruiting is likely to be from the middle to late wet season, so seedlings might first appear in the late wet season or early dry season, in locations where wet ground is maintained throughout the wet season. Without wet ground, taro seeds cannot germinate, and the seedlings cannot survive. At room temperature on a wet substrate, fresh taro seeds planted in the laboratory typically germinate two weeks after planting, without any dormant phase (author's observation). In the field, after dispersal on to wet ground surfaces, it is likely that taro seeds germinate after a similar period.

In the 1980s, while conducting field surveys in Australia and Papua New Guinea, I became interested in various insect genera that have close co-evolutionary relationships with taro and other aroids (Part 3, this volume). Of special interest are the taro planthoppers (*Tarophagus* spp., Matthews 2003), taro grasshoppers (*Gesonula* spp., Rehn 1952, 1959; Amédégnato and Devriese 2008), and drosophilid flies in the genus *Colocasiomyia* (formerly *Drosophilella*) (Sultana et al. 2006). Earlier studies indicated great diversity and narrow host specificity among these flies (Carson and Okada 1982a, b; Toda and Okada 1983; Yafuso and Okada 1990), but it now appears that the pollinators

are not always restricted to one host plant species (Sultana et al. 2006, Takenaka et al. 2006). However, host switching by the flies is likely to have been influenced by human activities (for example, habitat modification, plant introduction, and transplantation) that lead to the juxtaposition of previously separate host plant taxa. In Okinawa, Japan, Miyake and Yafuso (2005) found that *Alocasia culcullata* (an exotic introduction of likely Chinese origin) is now pollinated by two *Colocasiomyia* species that are usually found on *Alocasia odora* (a plant that is generally considered native in Okinawa). It is possible that *Colocasiomyia* flies are involved in cross-pollination (hybridisation) among aroids generally. Further studies of insect pollinators will be important for understanding the natural and cultural history of taro and its wild relatives, and the possible role of hybridisation in the domestication history of taro.

18.4 Historical Linguistics and Phylogeography

Taro, along with other aroid crops (Matthews 1995), has a strong but not exclusive association with the spread of the Austronesian language family. Names for taro, or varieties of taro, in Māori (an Austronesian language) are noted in Appendix 9. Since taro is a staple crop in many Pacific islands, reconstructing names for taro and taro-related terms in hypothetical Austronesian proto-languages has been significant for discussions of Oceanic culture history (e.g. Pawley and Green 1973, 1985; Blust 1984–85; Ross 1988; Li 1994; Wolff 1994; Ross et al. 1998). Early Austronesian-speaking societies are believed to have known and used taro, but linguistic evidence does not positively indicate that taro was present in the proto-Austronesian vocabulary (Blust 1984–85, Bellwood 1997: 242). If Austro-Asiatic names for taro are accepted as cognates for the Austronesian names (as suggested by Blench 2012), then it may be necessary to consider the possibility of cross-family borrowing in either direction, depending on where, geographically, taro is likely to have had a longer association with people as a useful plant.

Few linguistic studies have focused solely on taro and taro-related terms: the only examples may be Portères (1960), Kikusawa (2000), and Blench (2012). There has been no published attempt to record and collate data on the names and related terms in all language families in the regions of Asia and the Pacific where taro is wild or has been long cultivated. How vernacular names for taro vary between the wild and cultivated forms is hardly known, and it is not easy, at present, to relate the emerging phylogeographical understanding of taro (and its close wild relatives) with the emergence, diversification, and spread of names and terms associated with the plant. In Chapter Sixteen, two main directions of domestication were suggested, one leading to temperate adapted forms of taro and beginning in the Himalayan mountain region, and a second beginning in possibly multiple regions within the wet tropical zone extending from India and Southeast Asia to New Guinea. These are all key regions to begin analysing the names of taro, and the difficulty of the task is well illustrated by Blench (2012), who notes, for example, that Northeast India is a region of high lexical diversity in the names for taro, forming a complex of apparently unrelated terms. He suggests that this may reflect local transfers to taro of terms originally applied to wild aroids in the region.

Since cultivated taro, wild taro and closely related wild species are distributed from Himalaya to Vietnam, China, and Taiwan, lexical diversity and complexity in taro names and related terms is likely to exist over a much larger geographical range than that already indicated. Blench (2012) has surveyed languages in most regions where tropical cultivated taros are likely to have originated. The region where cool-adapted (temperate) cultivars of taro are likely to have originated, from Himalaya to the eastern mountain slopes in southern and central China, is only partially covered. No comparison has been made, so far, of Austronesian names and related terms for cultivated taro (*C. esculenta*) and wild taro (*C. formosana*, Figure 18.5) in Taiwan.

18.5 Theories of Origin, Domestication and Dispersal

Genetic diversity in taro has mainly been explored through studies of cultivars held in living research collections. Yoshino and his colleagues analysed isozyme variation and focused on relationships between triploid and diploid cultivars in Yunnan and Nepal. The results indicated that the triploid cultivars in Yunnan are most closely related to diploid cultivars in Yunnan, and that triploid cultivars in Nepal are most closely related to diploid cultivars in Nepal. The derivation of triploids via unreduced gamete production was also confirmed (cf. Chapter Fifteen). Tahara et al. (1999), Ochiai et al. (2001), and Yoshino (2002) concluded that since the triploids are derived from diploids, the diploid taros in Nepal and Yunnan must have differentiated as separate gene pools in each area, before the triploids arose (Figure 18.6). This implies that domestication began in breeding taro

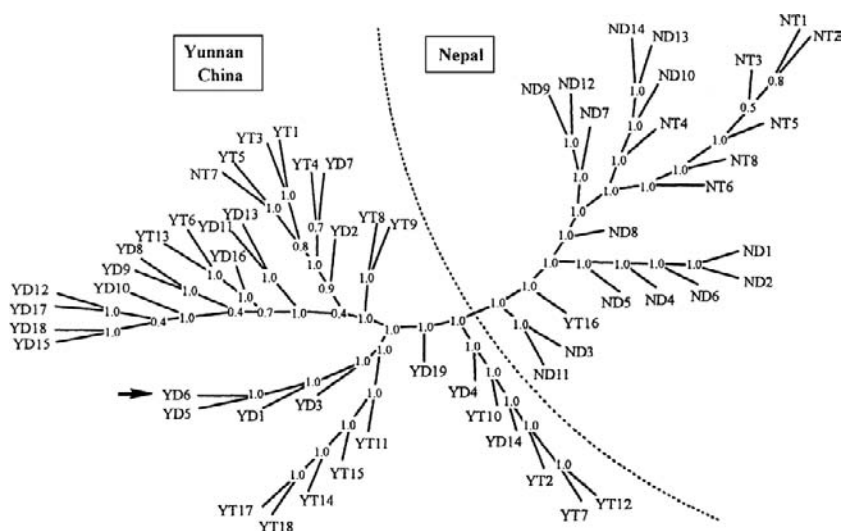


Figure 18.6 Consensus phylogenetic tree obtained after Wagner parsimony analysis of isozyme variation data of taro. Each labelled tip represents a single tested plant. D=diploid, T=triploid. Since no outgroup was known among the accessions, the tree is unrooted, though YD6 (arrowed) served as an outgroup for the purposes of calculation (from Yoshino 2002 and Tahara et al. 1999).

populations in the separate regions of Nepal (Himalaya) and Yunnan, China (near-Himalaya). The results are consistent with ethnobotanical observations (Xu et al. 2001) cytological surveys by Zhang and Zhang (1990, 2000), and the evidence for two principal routes of movement of cultivars into Japan, from Southeast Asia and mainland China (Matsuda 2002).

In surveys focused on cultivars in Southeast Asia and the Pacific Islands, Lebot and his colleagues have shown that the diversity of taro in remote Oceania is very narrow relative to that found in Melanesia and Southeast Asia, where two distinct gene pools can be seen (Kreike et al. 2004; Lebot et al. 2010). The observed decline in cultivar diversity, within one species, from west to east in the Pacific, mirrors a general, species-level decline in pre-European crop introductions from west to east (Matthews 2007; Whistler 2009). Since wild and cultivated taros may breed with each other, it is of interest to know where the eastern limit of the natural range of taro is located. In an analysis of genetic variation in wild and cultivated taros on islands in the Vanuatu group, AFLP data suggested close similarity between cultivars and most wild taros (Caillon et al. 2006). Despite the observed production of fruit and seed by wild taros, and the observation of birds (potential dispersal agents) eating taro fruit, the presence or absence of natural wild populations of taro in Vanuatu remains uncertain. The eastern limit of the natural range of taro may lay further to the west. Lebot et al. (2010) analysed isoenzymes (representing the nuclear genome) in a very large survey of 2,081 cultivars from seven countries in Southeast Asia and Oceania. The two cultivar gene pools are very tightly clustered, and lie close to each other, while the few wild plants studied are distant and scattered (Figure 18.7). This suggests that the two cultivar gene pools, in aggregate, represent a small part of the overall diversity that exists in wild taro populations.

A study of chloroplast genome variation in taro is currently in progress (Ahmed et al. 2012, 2013). The initial results suggest that chloroplast genome diversity in taro is large, when wild plants are included in the comparison. This is consistent with the nuclear genome data (zymotype analysis) summarised above.

In Figure 9.2 (also shown in Matthews 1991), I indicated the global distribution of taro in cultivation, likely natural range of wild taro, and the distributions of other *Colocasia* species for which distribution data were available (*C. affinis*, *C. fallax*, *C. gigantea*). These other species provided a geographical reference point for the natural origin of *C. esculenta* as a natural species, and two schemes regarding the evolution, dispersal and domestication of taro were proposed. In the first scheme (Figure 16.1), the selection and dispersal of taro by humans began with starchy wild-types that evolved and dispersed naturally within a range restricted to mainland Southeast Asia. This single-origin scheme followed the suggestion by Hotta (1983) that root crops developed where species hibernated naturally in response to either seasonal dry periods or seasonal cold periods (see also Hutterer 1983; an alternative view in Hather 1996; Hotta 2002). It was thus assumed that starch was a target for the initial selection, use, dispersal, and cultivation of wild forms.

In the second scheme (Figure 16.3), selection and dispersal of taro by humans began with non-starchy wild-types of wide natural occurrence, in tropical and warm temperate

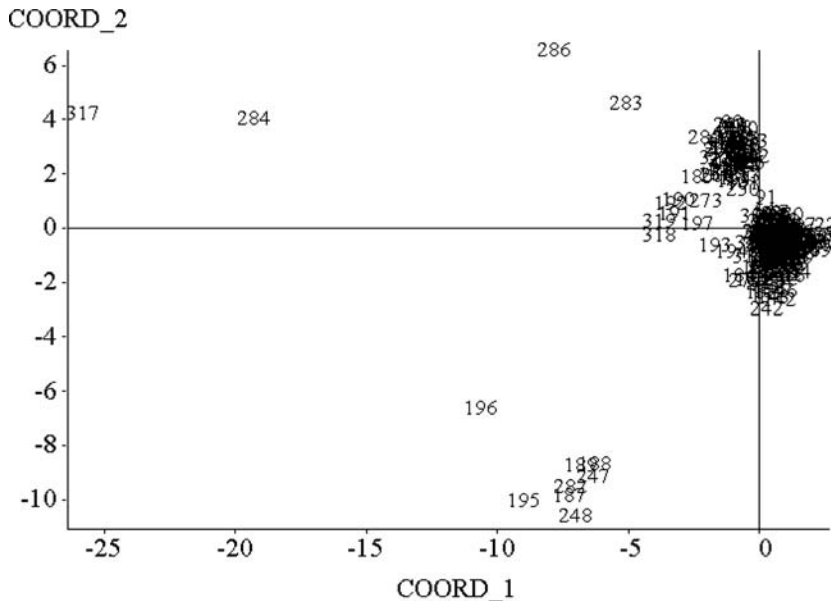


Figure 18.7 Principal components analysis of isozyme variation (zymotypes) in 2081 cultivars from seven countries in Southeast Asia and Oceania (from Lebot et al. 2010).

zones, respectively. In this case, it was suggested that starchiness increased in multiple areas of domestication after breeding and selection in early farming systems. More specifically, domestication may have begun in early swidden systems or nursery plantings (Matthews 1995). Such loosely controlled places provide obvious opportunities for breeding among cultivar assemblages in warmer climatic regions. Offspring growing from seed in fallow gardens or in nurseries might eventually be incorporated into active gardens, or provide planting materials for active gardens. Since proposing these contrasting theories, new evidence has become available regarding the diversity and distribution of wild *Colocasia* species, the economic uses of wild taro, and the ecological requirements for breeding populations of taro. Caillon et al. (2006) have reported the breeding of taro in populations apparently derived from cultigens, in Vanuatu, and the subsequent propagation of seeds by local farmers who had lost their vegetative planting materials. Botanical exploration in Southeast Asia and southern China has dramatically increased the number of known wild species of taro (cf. Hay 1996; Hsu et al. 2000; Long and Liu 2001; Yin et al. 2004; Ara and Hassan 2005; Cai et al. 2006; Yin 2006; Long and Li 2008; Li and Boyce 2010; Gogoi and Bosah 2013; Matthews and Nguyen 2014) (see *C. yunnanensis*, Figure 18.8, for example). This in turn suggests a huge expansion in the range of unexplored territory in which further wild species of *Colocasia* are likely to be found, from mainland and island Southeast Asia, to western Himalaya and southern or central China. Within the expanded region of reported diversity, further unreported species are likely to exist in remote mountain valleys, at elevations similar to



Figure 18.8 *C. yunnanensis* Long and Cai at approx. 2000 m above sea level, near Sapa, northern Vietnam (2012, with D. V. Nguyen)

those where many recent discoveries were made (c. 400–4,000 m a.s.l.). At such elevations, there are still many areas that cannot be reached by road and that remain to be explored. Leaving aside all uncertainties, I will now consider the diversity and distribution of wild *Colocasia* species in relation to the theories of origin, domestication and dispersal discussed earlier.

The evolutionary origin of taro (*C. esculenta*) was previously thought to be in the vicinity of northeastern India, where the greatest diversity of other wild *Colocasia* species was known (Figure 9.2), and thus where a common ancestor may have been located. Now it is known that wild *Colocasia* species are spread over a much larger area, and mainly in mountains, throughout the northern monsoon region of Asia (Figure 16.2). The obvious diversification of *Colocasia* species in montane regions of Asia may reflect

a long natural history of evolution in response to tectonic uplift and climate change, over millions of years. The evolutionary origin of taro must be sought over this larger area, and the lower montane zone may be the most likely area to look, given the eventual spread of taro into tropical lowland regions.

18.6 Looking Back and Looking to the Future

Previous chapters in this book have presented very local to very broad images of the natural and cultural history of taro, all as part of an attempt to look back in time at the origins and dispersal of the crop. The great diversity of wild and cultivated forms of taro is still largely unmapped and undescribed, along with the diversity of cultural practices and meanings associated with the plant. The natural and cultural history of taro must be explored on foot, through swamps, along rivers, over mountains, into kitchens, and into the fields of farmers. Such work cannot be accomplished without guides, interpreters, hospitality, and the kindness of strangers. In my own experience on this trail, the appreciation of plants has been a unifying language for building new relationships with many different people. Perhaps it has always been this way, in the journeys and encounters that carried our ancestors, and taro, around the world.

As an ethnobotanist and crop historian, I am always asking how we can learn about the past of taro, especially in situations where the trail is most difficult to follow: looking back towards the distant past, and in societies where interactions between the plant and people are most complex. More by good fortune than good planning, my own journey began in places where the natural and cultural history of taro is relatively simple, in historical terms, in New Zealand and northern Australia. In Papua New Guinea — a more complex environment — I focused on wild populations of taro, which might represent progenitors for cultivated taro, or descendants, or a mixture of both, thanks to the clonal and sexual nature of the plant. As a species, taro has always been a reticulate, mobile, and evolving network, and it may have been tangled with a reticulate, mobile, and evolving network of human communities since long before the emergence of agriculture. Despite all the historical complexity, the division of cultivated taro into tropical and temperate forms is clear. This points to potential value in the future: the diversity that already exists in cultivated taro can be used as part of human adaptation to changes in climate (warmer, colder, or less stable) and crop production.

As we learn more about the natural and cultural history of taro, we can learn more about its potentials for future utilisation and enjoyment — as a wild and cultivated food or fodder plant, source of medicine, ornamental plant, and as a plant with different practical and cultural value in each area where it is grown and used. The potential of taro as a source of food security in China was stated in dramatic but realistic terms in the mid-16th century, by Shengzheng Huang (Huang 2012: 50–51):

‘...taro can help the country get through famine caused by a bad year for agriculture. Nowadays people seldom heed this advice. The latter generations have abandoned their senses, and it is too late when floods, droughts, storms, insects, frost and hailstorms hit.

People starve to death and their bodies litter the streets. Having the knowledge and ignoring it, and thus leading to annihilation, is the ultimate crime for a ruler. This advice should always be remembered.'

In Chapter Seventeen I noted a recent and understandable focus on issues of immediate practical concern for the production of taro in different countries and regions. Fundamental historical understanding of the crop will make it easier to imagine a wider range of goals for practical development of the crop. Whimsical development also has serious value, as flower growers and breeders know, and is a path that favours serendipity in learning about the plant. Any gardener, school teacher, or cook can participate in the development of taro by growing the plant, enjoying its ornamental qualities and food value, and telling others what he or she has learned.

If adaptation to climate change becomes our primary goal because of global warming, cooling, or instability (Taylor 2009), then we should consider how to use existing kinds of taro effectively, and how to develop new kinds of taro suitable for diverse combinations of water supply, temperature, humidity, soil fertility, growing season, day-length, total hours of sun, cropping system, culinary value, nutritional value, and disease resistance or tolerance. All of these factors, and more, are significant whenever an attempt is made to preserve or improve the plants that we live with.

We know how to feed the world: bring our present and future resources into balance with our present and future demands (Smil 2004; Tudge 2007). Since the world is always changing, 'sustainability' must be a dynamic balance, one in which we are constantly adapting to new challenges. We can do this on our own terms, or we can do this, less wisely, on terms imposed by the limits and uncertainties that we face. In all likelihood, we will only partly succeed in avoiding future food disasters, no matter how well we understand ourselves and the world. Our ignorance is unlimited. That is the magic and tragedy of science, and human knowledge generally. There is always more to learn.

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APPENDICES

The present section includes: appendices from Matthews (1984) (Appendices 1–11), appendices from Matthews (1990) (Appendices 12–20), an unpublished protocol for sampling wild taro sites (Appendix 21), a guide to assist the survey, description, and identification of wild-type taro (Appendix 22), and an unpublished flyer describing the introduction of two Japanese cultivars to New Zealand (Appendix 23).

Appendix 1. Early correspondence

In this appendix, correspondents of the period 1981 to 1983 are listed alphabetically, together with a brief description of the subject of correspondence. It is hoped that access to the correspondence made during the present research will help in future studies of taro, botanical or ethnographic. The letters themselves were first filed with the Herbarium, Department of Botany, University of Auckland, and were later transferred to the Herbarium, Auckland War Memorial Museum.

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| Adams, N. M. | National Museum of New Zealand, Private Bag, Wellington. 3.3.81 List of taro specimens held at the National Museum Herbarium. |
| Arditti, J. | University of California, Irvine, Department of Developmental and Cell Biology, School of Biological Sciences. 2.4.82 Unable to assist on questions about taro cytology or biochemistry. |
| Arnott, F. D. | Hauraki Gulf Maritime Park Board, Department of Lands and Survey, P. O. Box 5249, Auckland. 10.12.81 Permit to visit Little Barrier Island. 7.1.82 Permission to remove taro specimens from Little Barrier Island. |
| Baker, T. | Auckland, July 1983 Enquiry about growing taro in the Far North (phone call). |
| Barber, I. | c/o Department of Anthropology, University of Auckland, Private Bag, Auckland. Oct. 1983. Reports information from Māori informants. |
| Barker, M. C. | Herbarium, Department of Botany, University of Canterbury, Christchurch. 3.8.81 No specimens of New Zealand taro in the Herbarium. |
| Bawden, P. | Royal Oak, Auckland. 25.1.83 Reports taro locations in Whangaroa area. 3.2.83 Further information on a taro site. |

- Bayliss, G. University of Otago, Dunedin. 5.4.57 Reports taro at Omaio Bay, East Cape. (Letter to J A Rattenbury, Department of Botany, University of Auckland).
- Bellingham, P. Puketi Forest Headquarters, P. O. Box 249, Kaikohe. 22.2.83 Reports taro sites in Northland. 22.1.84 Reports fruiting of aroid (arum lily) at Ngawha.
- Botany Department University of Auckland. April 1983 Public response to Open Day display: offers of information on taro.
- Braggins, J. E. c/o Department of Botany, University of Peradeniya, Peradeniya, Sri Lanka. 19.10.82 References and some comments on Southeast Asian taro. Contact names for Indonesia.
- Brook, P. J. Plant Diseases Division, Department of Scientific and Industrial Research, Private Bag, Auckland. 8.12.81 Offer of ground space for growing an experimental taro plot.
- Burns, B. Department of Lands and Survey, Auckland, 1.6.83. Reports taro sites on Coromandel Peninsula.
- Chamberlain, T. Manganese Point Road, Tamaterau, R D 4, Whangarei. 2.4.82 Gives history of taro in his garden and reports a nearby site. (Source of AKL 34, diploid taro cultivar).
- Clark, F. Waitara, Taranaki. Reports taro in New Plymouth gardens and at a very old Māori settlement area on the North Taranaki Coast.
- Connor, J. c/o Department of Anthropology, University of Auckland. 10.8.82 Gives names of people met during May 1982, field trip with P Matthews.
- Cooper, R. C. Whangaparaoa, Auckland. 29.9.81 Sends slides from his work on New Zealand taro during the 1950s and early 1960s. Comments on New Zealand taro.
- Coster, J. Archaeologist, Department of Lands and Survey, Auckland. 17.11.83 Reports taro sites in the Far North.
- Data, E. S. Philippine Root Crop Research and Training Center, 8 Lourdes Street, Pasay City 3129, Philippines. 3.6.82 Information on a symposium and contact addresses.
- Dawson, J. Botany Department, Victoria University of Wellington, Private Bag, Wellington. 17.12.82 Offer to assist with taro research while visiting Tahiti and Hawai'i.

- Derby, M. c/o Post Office, Mangamuka Bridge, Hokianga. 12.7.82 Discusses possibility of local assistance with taro research by the Hokianga Experimental Training Nursery. Asks for information on taro for the *Tai Tokerau Co-operatives Information Exchange* magazine.
- Diongzon, Jr, O. C. E. Plant Breeder, Visayas State College of Agriculture, Philippine Root Crop Research and Training Center, 8 Lourdes Street, Pasay City 3129. 8.10.82 Sends abstract and methods of her/his study "Cytology and Morphology of Edible Aroids". Comments on corm shapes.
- Doolin, E. R. Waikato Regional Committee, New Zealand Historic Places Trust, c/o Hamilton Teacher's College, Private Bag, Hamilton. 13.3.81 Copy of letter to Botany Division, Mount Albert Research Center, D.S.I.R., Auckland. Sends taro sample collected from Aotea Harbour. Comments added by Alan Esler, Botany Division, Mount Albert.
- Esler, A. Botany Division, D.S.I.R., Mount Albert Research Center, Auckland. February 1982. Provides reference to unpublished D.S.I.R. report giving taro locations in the Bay of Plenty.
- Eyles, J. R. Director, West Coast Historical Museum, P. O. Box 1S5, Hokitika. 3.11.82 Reports no local knowledge of taro on the South Island West Coast. Gives origin of taro grown at Kelson (Te Kaha, East Coast, North Island).
- Fuller, G. Curator, Pukekura Park, Parks and Recreation Department, Private Bag, New Plymouth. 29.11.82 Describes taro growing at Pukekura Park and contact addresses in New Plymouth. 13.4.83 Gives descriptions of taro material sent to Auckland and address of someone who might know of taro on the Whanganui River.
- Gaillard, J. Project Secretary, International Foundation for Science, Sibyllegatan 47, S-11442, Stockholm. 20.4.82 Sends IFS Report No. 11. Gives contact address for Philippines.
- Gardiner, J. Chief Ranger, Bay of Islands Maritime and Historic Park Board, Box 134, Russell. 23.8.82 Offer of assistance with sea transport for fieldwork.
- Gardner, R. Auckland. 16.1.82 Reports taro sites. Asks for planting material for glasshouse. 22.3.82 Comments on taro grown in Auckland city for greens. Gives a reference. October 83 Gives reference on pig consumption of taro.
- Godley, E. Director, Botany Division, D.S.I.R., Private Bag, Christchurch. 5.8.81 Reports absence of taro in the Botany Division Herbarium.

- Gollifer, D. Department of Agricultural Research, Private Bag 0033, Gaborone, Republic of Botswana. 30.9.81 Sends xeroxed parts of his PhD thesis on fungal pathology of taro.
- Goodin, V. & M. Managers, Moturoa Island, Private Bag Paihia. 17.3.83 Reports taro absent from island. Reports other locations with taro.
- Gordons Jane Nelson Place, Whangarei. 23.5.83 Letter to Molly Taylor (Department of Botany, University of Auckland). Reports taro in Whangarei area.
- Harlow, R. Department of Linguistics, University of Otago, Box 56, Dunedin. 21.10.83 Computer research for Māori names for taro in the three volumes of poems/songs of Ngaa Mooteatea.
- Hatch, E. D. Laingholm, Auckland. Reports taro on the Manukau Harbour coast.
- Hayward, M. T. Noxious Plants Officer, Bay of Islands County Council, P. O. Box 11, Kawakawa. 6.5.82 Offers information, invites visit.
- Heginbotham, M. Woodlands Road, Opotiki. 14.9.82 Is unable to give precise locations for taro reported in unpublished manuscript (*Wild Plants of Ohope to East Cape*) private report to Botany Division, D.S.I.R., 1979). Gives other locations and sends live samples. 20.12.82 Invitation to visit, people to contact at Torere, East Cape.
- Hensley, V. R D 4, Kaitaia. 29.1.82 Reports taro sites in the Far North.
- Hooper, A. Department of Anthropology, University of Auckland, Private Bag, Auckland. 17.3.82 offers information on *Cyrtosperma* in the Tokelau Islands.
- Hovell, J. Te Aute College, Pukehou, Hawkes Bay. 6.12.82 Gives contact addresses for Coromandel Peninsula and East Cape, and Easter Island. Comments on history and present cultivation.
- Jones, K. Staff archaeologist, N.Z. Historic Places Trust, Private Bag, Wellington 1. 19.10.82 Sends samples and gives locations. Reports absence of taro at Tolaga Bay. 11.4.83 Reports taro sites on East Coast and remarks on present attitude to taro there.
- Knowles, R. Lower Weld Road, R D 4, New Plymouth. 28.11.83 Offers to send taro from a Whanganui River Māori settlement. 24.1.84 Sends variant RR sample.

- Krumins, G. Canoe Camping Limited, 112 Owhiro Bay Parade, Wellington
2. 8.7.82 Reports taro sites along Whanganui River.
- Laundon, G. Plant Health and Diagnostic Station, Private Bag, Levin.
7.10.81 States that no permit is required to import taro into
New Zealand. Would like to be informed should reasons be
found for imposing a restriction.
- Leach, H. Department of Anthropology, University of Otago, Private
Bag, Dunedin. 26.7.82 Letter to D. Sutton, Department of
Anthropology, University of Auckland. Comments on N.Z.
taro. 18.4.83 Historical references and draft from her
forthcoming book *A Thousand Years of Gardening in New
Zealand*. 2.2.84 Comments on interpretation of taro
distribution and names.
- Leahy, A. Mount Eden, Auckland. 3.5.82 Reports taro sites in Bay of
Islands and Bay of Plenty, and taro flowering.
- Lewis, M. Department of Zoology, University of Auckland, Private Bag,
Auckland. 26.5.83 Gives identification of beetle commonly
found in taro flowers.
- Lord, W. B. Bay Road, Waiheke Island, Auckland. 11.1.82 Describes his
method of growing taro.
- Lusk, P. No. 1 Road, Westport, South Island. 26.3.82 Reports South
Island taro sites.
- McConnell, R. Te Araroa, East Coast. 2.6.83 Notes on taro in the East Coast
– East Cape areas. Reports flowering.
- Matthews, P. J. Department of Botany, University of Auckland, Private Bag,
Auckland. 10.1.83 Advertisement for field assistant.
- Mizen, P. Titikaveka, Rarotonga, Cook Islands. 26.9.83 Reports taro
absent from Ahuahu Island, New Zealand.
- Navaratnam, S. J. Department of Health, P. O. Box 100, Woden, A.C.T. 2606,
Australia. 26.10.83 Letter to D E Yen: permission for import
of New Zealand taro.
- Pollack, N. J. Department of Anthropology , Victoria University of
Wellington, P. O. Box 196, Wellington. 6.4.83 Describes her
ethnographic research on the use of food plants in the Pacific.
- Prickett, N. Auckland Institute and Museum, Private Bag, Auckland.
21.4.82 Advice for writing NZAA Newsletter article and an
address for taro site information.
- Rau-Kupa, Mrs. Raleigh Street, New Plymouth. 25.2.83 Taro and information
on history, use and cultivation.

- Raupo Trust R D 3, Kaitaia. 1982 Asks for information on growing taro.
- Reid, M. Taranaki Museum, P. O. Box 315, New Plymouth. 20.12.82 Has no information.
- Reynolds, K. Anzac Road, Whangarei. 9.10.81 Reports taro sites, history and names. 3.5.82 Reports taro sites and flowering in the Far North.
- Rickard, J. Overseas Development Administration, Tropical Products Institute, 56–62 Gray's Inn Road, London WC1X 8LU. 3.12.82 Sends and asks for information on taro.
- Robinson, S. Museum Historian, Gisborne Museum and Arts Centre, P. O. Box 716, Gisborne. 26.11.82 Gives contact addresses for East Coast area.
- Rogers, G. Department of Anthropology, University of Auckland, Private Bag, Auckland. 4.3.82 Notes flowering of Auckland City taro. 3.2.83 Notes on frost damage to cultivated taro in North Auckland.
- Ross, M. Scanlan Street, Grey Lynn, Auckland. 25.1.83 Reports taro site at Hunua Gorge.
- Sheward, A. Rotorua. 18.1.84 Reports distribution and names of taro.
- Smith, W. P. Whangarei. 13.4.83 Reports Whananaki taro sites, Northland-Asks for information.
- Spriggs, M. Department of Anthropology, University of Hawai'i at Manoa, 2424 Maile Way, Honolulu, Hawai'i 96822. 30.11.81 Gives suggestions for the N.Z. taro study, references and contact addresses.
- Stevenson, G. Ploustone Lane, Bromley, Kent BR 1 3JE, England. 16.9.83 Doesn't have her papers or notes with her. (Ref. "Botanical evidence linking the New Zealand Māori's with New Caledonia and the New Hebrides", *Nature* 276, 704–5).
- Strauss, M. S. Department of Botany, College of Arts and Sciences, Northeastern University, 360 Huntington Avenue, Boston, Massachusetts 02115, U.S.A. 20.5.83 Sends reprint. Asks for plants. 5.12.83 Sends pre-publication xerox of a review: Michael S Strauss and Daniel C Sheirer, "Morphology of taro, *Colocasia esoulenta* (ARACEAE)" submitted to *Economic Botany* 12/83.

- Sutherland, J. F. Department of Lands and Survey, Map and Photo Sales, Private Bag, Charles Fergusson Building, Wellington 1. 8.11.83 Cost of an aerial photograph of Torere East Cape. Information about aerial photo sets.
- Sutton, D. G. Department of Anthropology, University of Auckland, Private Bag, Auckland. 3.8.82 Ethnographic references.
- Tangiwai, P. Te Awamutu. 7.6.83 Information on use, names, history and cultivation of taro. Asks for information.
- Taylor, M. Hirini Street, Gisborne. 18,12.82. Remembers taro thirty-two years ago at Te Araroa.
- Thain, E. M. Director, Overseas Development Commission, Tropical Development and Research Institute, 127 Clerkenwell Road, London EC1R 5DB. 12-5.83 Can't help re taro. Describes the work of the T.D.R.I.
- Thyrme, A. F. Executive Officer, The Royal Society of New Zealand, Science Centre, 11 Turnbull Street, Private Bag, Wellington. 1.11.82 Research Grant from the Mappin Trust. 16.8.83 Acknowledges receipt of application for a second Grant. 12.12.83 Sends cheque for second Grant.
- Twohill, N. Thames. 27.6.82 Reports taro along the Thames coast. Comments on effects of winter on plants.
- Vincent, D. Editor, *Northland Age*, P. O. Box 45, Kaitaia. 26.4.82 Reports taro sites and history for the Far North. 1.9.82 Reports taro sites and history for the Far North again.
- Walls, G. Botany Division, D.S.I.R., Private Bag, Christchurch. 4.5.82 Reports general absence of taro from the Nelson and Marlborough areas. Gives South Island contact address.
- Walls, J. Takaka, Golden Bay. 22.9.83 Reports South Island taro, ethnographic references, and South Island contact address.
- Walton, A. Archaeology Section, New Zealand Historic Places Trust, Private Bag, Wellington. 10.5.82 Sends computer list of taro sites from NZAA site recording scheme.
- Wang, J.-K. Department of Agricultural Engineering, University of Hawai'i at Manoa, 3050 Maile Way, Honolulu, Hawai'i 96822. 28.3.83 Information on projects, Hawai'i taro collection and flowering.

- Watson, J. Manager, Imported Fruit Department, Turners and Growers Limited, P. O. Box 56, Auckland. 2.7.82 Gives history of taro imports to New Zealand. Also see J. Watson (1979) in Plucknett (ed.) *Small-Scale Processing and Storage of Tropical Root Crops* pp. 151–65.
- Whitmore, F. W. Registrar, Plant Varieties Office, P. O. Box 24, Lincoln, New Zealand. 12.9.83 States legal situation under the Plant Varieties Act 1973 regarding taro.
- Williams, D. B. Root Crops Development in the Pacific Project, F.A.O., P. O. Box 890, Apia, West Samoa. Outlines aims of the Project regarding taro.
- Wright, A. E. Botanist, Auckland Institute and Museum, Private Bag, Auckland 1. 15.3.83 Programme for Offshore Islands of K.E. New Zealand symposium. 9.11.83 Reports taro grown at Rotorua under traditional names.
- Wright, P. Secretary, Waikato Regional Committee, New Zealand Historic Places Trust, Hamilton. 2.6.83 History of taro at Raukumara, Aotea Harbour. Reports that taro is common in the Waikato area.
- Yen, D. E. Department of Prehistory, Research School of Pacific Studies, Australian National University, P. O. Box 4, Canberra ACT 2600. 3.5.82 Comments on Oceanic, Australian and New Zealand taro. 4.11.82 Reports chromosome counts of Australian and Papua New Guinean taro. Further information on his work with New Zealand taro including stolon information. 28.3.83 Further comments on work with N.Z. taro; Māori naming, flowering.

Appendix 2. New Zealand taro site records

The site records are held in the Herbarium, Department of Botany, University of Auckland (later transferred to Auckland War Memorial Museum). An example is given below. Explanation of terms:

Botany Department Site Number: Map number (NZMS1 Series except for NZMS 259 Great Barrier Island and Little Barrier Island) followed by the individual site number in sequence of recording.

Grid reference: NZMS map grid reference, Easting and Northing, to 100 yards (91 m).

Variant: Informal nomenclature for three variants of New Zealand taro, RR, GR, and GP described in Chapter Ten. Variants other than RR, GR or GP are identified by their live-plant collection number, prefixed by 'AKL', in the Auckland live-plant collection. The collection is described in Appendix 3.

Site Description: Full definitions of site categories are given in Chapter Twelve.

Site Record (example):

NEW ZEALAND ARCHAEOLOGICAL ASSOCIATION SITE RECORD FORM (NZMS1) NZMS 1 map number N61 + 60 NZMS 1 map name Te Kaha NZMS 1 map edition 2nd, 1970		NZAA/NZMS 1 SITE NUMBER DATE VISITED 21.1.83 SITE TYPE TARO SITE NAME: MAORI ? OTHER	
Grid Reference Easting <input type="text" value="117"/>		Northing <input type="text" value="514"/>	
1. Aids to relocation of site (attach a sketch map) <i>On hill above the school</i> <i>B.O.N61+60/3</i>			
2. State of site and possible future damage			
3. Description of site (Supply full details, history, local environment, references, sketches, etc. If extra sheets are attached, include a summary here) <i>In gardens of Mr Tawhii, and his neighbours who got them from Opatiki</i> <i>RR, Garden, ?</i>			
4 Owner <i>Mr Tawhii</i> Address <i>1/6 Te Kaha P.O.</i>		Tenant/Manager Address	
5. Nature of information (hersay, brief or extended visit, etc.) <i>visit</i> Photographs (reference numbers, and where they are held) Aerial photographs (reference numbers, and clarity of site)			
6 Reported by <i>P. Matthews</i> Address <i>1/6 Dept of Botany</i> <i>Univ A, Jan 83</i>		Filekeeper Date	
7. Key words			
8. New Zealand Register of Archaeological Sites (for office use) NZHPT Site Field Code			
<input type="text"/> Type of site <input type="text"/> Local environment today <input type="text"/> Land classification		<input type="text"/> Present condition and future danger of destruction <input type="text"/> Security code <input type="text"/> Local body	

Botany Dept. site number	Grid ref. E.N	Variant	SITE DESCRIPTION			Wild
			Garden			
			Cultiv.	Non-cultivated		
non-derelict	derelict					
N1&2						
1	374 452	RR	?			
2	352 515	GP				X
3	43? 51?	?	?			
4	314 455	?				X
5	466 452	?	?			
6	352 510	* GP, GR				X
7	344 523	?	?			
8	65 481	?	?			
N3&4						
1	534 118	* GR	?			
2	515 164	GR				X
N7						
1	144 874	GP	?			
2	84? 00?	?	?			
3	047 878	?	?			
4	051 865	?	?			
5	03? 90?	?	?			
6	911 986	?	?			
N8						
1	210 846	?	?			
2	283 881	RR				X
3	443 829	RR				X
4	442 837	RR				X
5	446 843	RR				X
6	352 823	?	?			
7	277 886	?	?			
8	444 832	RR				X
9	444 842	RR				X
10	443 836	RR				X
11	440 839	RR				X
12	444 844	RR				X
13	222 819	RR	?			
14	340 833	GP				X
15	284 877	?	?			
16	282 877	?	?			
N9&13						

1	*	724 503	GP			X
2		723 504	GP			X
3		722 505	RR			X
4		724 533	RR		X	
5	*	684 599	GP			X
6		675 605	* GP, GR			X
7		660 603	GP, GR			X
8		618 616	GP			X
9		605 614	GP			X
10		597 617	GP			X
11		626 609	GR		X	
12		712 514	?	?		
N10						
1		864 639	GR			X
2		822 666	?	?		
3		78? 79?	?	?		
4		045 576	GR		X	
5		035 583	?	?		
6		583 049	RR			X
7		705 622	RR			X
8		777 744	?			X
9		779 742	?			X
10		785 741	?			X
11		784 737	?			X
12		774 738	RR			X
13		776 740	RR			X
14		778 739	RR			X
15		776 734	RR			X
16		776 694	RR			X
17		045 693	RR			X
18		054 586	RR			X
19		14? 71?	?	?		
N11						
1	*	604 658	?	?		
2		548 523	GP			X
3		474 695	?	?		
4	*	428 768	RR			X
5	*	436 775	?			X
6		622 637	RR			X
7	*	430 759	RR			X
8		518 694	?	?		
9		52? 67?	RR	?		
10		318 699	?	?		
11		636 534	RR			X

12	300?	?	?			
13	296 790	GP	?			
14	318 699	?	?			
N12						
1	797 542	RR			X	
2	811 614	?	?			
3	714 602	?			X	
4	718 584	?	?			
5	772 565	RR				X
6	810 609	RR				X
7	69? 57?	?				X
N14						
1	107 401	RR				X
2	872 313	RR	?			
3	812 293	GP			X	
4	895 370	?	X			
5	MISSING					
6	843 300	?	?			
7	970 394	GR	?			
8	003 324	RR	?			
9	108 235	GR		X		
10	100 242	RR	X			
11	048 274	RR	X			
12	979 259	GR, RR		X		
13	975 266	RR	X			
14	929 228	GP		X		
15	977 253	RR	?			
16	043 281	RR	?			
17	094 247	RR	X			
18	118 256	RR		X		
19	114 267	RR				X
20	098 399	GR, RR		X		
21	057 343	RR		X		
22	086 362	RR		X		
23	106 380	RR	?			
24	134 422	RR		X		
25	055 454	RR				X
26	078 479	RR				X
27	014 476	GR		X		
28	050 415	RR		X		
29	797 303	RR		X		
30	838 298	GR, GP				X
31	* 872 314	RR	?			
32	902 369	GR		X		

33	894 372	GR		X		
34	763 403	RR		X		
35	763 398	GR		X		
36	784 410	GR		X		
37	809 405	GR			X	
38	812 430	GR		X		
39	818 435	GR, RR		X		
40	760 348	RR	?			
41	754 362	?	?			
42	837 441	?			X	
43	752 413	?	?			
44	115 404	RR	X			
45	019 341	RR		X		
46	807 307	GP				X
47	100 242	RR		X		
N15						
1	440 406	?	?			
2	388 411	RR				X
3	368 399	RR				X
4	370 383	GP				X
5	371 343	RR	X			
6	317 343	RR		X		
7	382 468	GP,RR				X
8	418 476	RR				X
9	?	RR	X			
10	598 434	GP				X
11	461 404	RR		X		
12	* 595 426	GP				X
13	373 385	?	?			
14	583 385	?	?			
15	383 416	?	?			
16	647 260	?	?			
17	291 317	RR	X			
18	337 426	GP				X
19	336 407	GP		X		
20	345 407	RR				X
N16						
1	847 348	RR				X
2	888 300	RR				X
3	927 305	RR				X
4	855 312	RR				X
5	730 464	?	?			
6	733 448	?	?			
7	730 450	?	?			

8	740 453	?	?			
9	735 415	?	?			
10	868 424	RR	?			
11	967 204	?	?			
12	821 367	RR	?			
13	651 489	RR				X
14	653 491	RR		X		
15	792 450	RR	?			
16	783 517	RR	?			
17	955 264	?	?			
N18 & 22						
1	075 044	RR				X
2	943 144	GR, RR		X		
3	052 146	GR, RR		X		
4	024 147	RR	X			
5	006 153	RR		X		
6	907 187	GP		X		
7	024 147	RR		X		
N19						
1	220 902	?	?			
2	219 900	?	?			
N20						
1	035 975	?	X			
2	804 944	?	?			
3	818 923	?	?			
N23						
1	233 847	RR				X
2	274 857	?	?			
3	267 864	?	?			
4	233 847	RR	X			
N24						
1	943 898	RR	?			
2	937 893	RR, AKL34	?			
3	947 883	RR				X
N28						
1	045 581	?	?			
N33						
1	071 119	RR	?			

NZMS259						
1	345 740	RR		X		
2	607 838	?	?			
3	634 856	RR	?			
4	630 854	RR		X		
5	580 831	?	?			
6	669 853	RR				X
7	673 817	?	?			
8	623 843	?	?			
9	622 793	?	?			
10	671 696	?	?			
N34						
1	360 133	RR				X
2	363 116	RR		X		
3	324 177	RR	?			
N35						
I	973 001	RR		X		
2	953 012	RR		X		
N37						
1	875 844	?	?			
2	884 835	?	?			
3	900 813	?	?			
4	974 937	?	?			
5	952 722	RR				X
N39						
1	929 930	RR	?			
2	862 963	RR				X
3	966 759	RR		X		
4	974 872	GR		X		
5	908 936	RR				X
6	899 941	GR, RR		X		
7	856 966	RR				X
8	858 964	RR				X
9	957 998	RR	X			
10	643 708	?	?			
11	660 712	?	?			
N40						
1	074 866	RR		X		
2	049 827	RR		X		
3	064 804	?				X
4	032 800	RR		X		

5	036 904	?	?			
6	013 904	?	?			
N41						
1	093 423	?	?			
2	082 403	RR		X		
N42						
1	504 679	?	?			
2	16? 46?	RR	X			
3	109 414	RR	?			
N43						
1	557 681	RR	X			
2	558 678	RR		X		
3	553 677	RR				X
4	977 494	RR		X		
5	978 495	RR		X		
6	980 485	RR				X
7	943 533	RR				X
8	930 557	RR		X		
9	930 551	RR				X
10	956 603	RR		X		
11	970 603	RR	X			
12	972 604	RR			X	
13	989 596	RR			X	
14	987 601	RR			X	
15	947 606	?	?			
16	945 531	RR		X		
17	947 528	RR		X		
18	662 688	?	?			
N44						
1	000 457	?	?			
2	306 615	RR		X		
N46&47						
1	095 372	?	?			
2	103 368	GP				X
N60 & 61						
1	112 511	RR		X		
2	107 509	RR				X
3	117 514	RR	?			
4	131 525	RR			X	
5	142 548	RR				X

N62						
1	318 639	RR		X		
2	442 706	RR	X			
3	554 695	RR	X			
4	?	RR	?			
5	539 723	?	?			
M63						
1	708 664	RR	9			
2	928 529	RR	X			
3	791 616	RR		X		
4	792 615	GR		X		
5	758 606	RR	X			
6	767 611	RR		X		
7	764 610	RR		X		
8	716 647	RR			X	
9	773 613	GR, RR	X			
10	775 614	RR	X			
N65						
1	?	?	?			
N70						
1	102 493	?	?			
2	839 213	RR		X		
3	036 402	RR		X		
4	053 414	GP				X
5	914 253	RR	?			
N72						
1	836 462	RR	X			
2	833 458	RR			X	
3	837 460	RR		X		
4	803 426	RR			X	
5	806 425	RR				X
6	817 393	RR		X		
7	827 384	RR				X
8	784 390	RR			X	
9	724 306	RR	X			
N73						
1	343 186	9	?			
N78						
1	?	RR	?			
2	722 192	RR	?			

3	577 135	RR		X		
N80 & 81						
1	676 032	RR			X	
2	675 003	?	?			
N89 & 90						
1	673 713	?		X		
N109						
1	?	AKL 79	?			
2	?	AKL 80–82	?			
N121						
1	53? 60?	RR	?			
N131						
1	68? 19?	?	?			

Appendix 3. Auckland Taro Collection

Accessions in the collection of *Colocasia* sp. (living plants) made at the Department of Botany, University of Auckland, 1982–83. Unless otherwise stated, all accessions were *C. esculenta* (L.) Schott and were from within New Zealand.

Coll. No.	Variant/ Name/sp.	Accession Date	Discard Date	Collector	Coll. Date	Source - Botany Dept Site No.	Location
AKL							
1	RR	19.3.82	Mar-84	P Matthews	24.8.81	NZMS259/1	Te Waikohe Stream
2	RR	19.3.82	Mar-84	P Matthews	9.11.81	N41/2	Little Huia
3	RR	19.3.82	Mar-84	R Grace	Nov-81	—	Mimiwhangata
4	RR	19.3.82	Mar-84	P Matthews	7.1.82	N43/3	Wilma Road
5	RR	19.3.82	Mar-84	P Matthews	7.1.82	N43/2	Homai Road
6	RR	19.3.82	Mar-84	M Dye	Mar-82	N44/2	Hahei
7	RR	19.3.82	Mar-84	A Wright	Feb-82	N16/1	Mokau Stream
8	RR	19.3.82	Mar-84	I Lawlor	?	—	Coromandel Peninsula
9	RR	19.3.82	Mar-84	I Lawlor	?	N33/1	Ogles Creek
10	RR	19.3.82	Mar-84	I Lawlor	?	N78/1	Paerata Ridge
11	RR	25.3.82	Mar-84	E Matthews	23.3.82	N12/1	Whangamumu Harbour
12	Tonga Sea	8.4.82	—	R Fullerton	Mar-82	—	Totokoitu Research Station, Rarotonga
13	Mataga	8.4.82	—	R Fullerton	Mar-82	—	Totokoitu Research Station, Rarotonga

14	Sunday Fauli	8.4.82	—	R Fullerton	Mar-82	—	Totokoitu Research Station. Rarotonga
15	Niukini Ava'ava	8.4.82	—	R Fullerton	Mar-82	—	Totokoitu Research Station. Rarotonga
16	RR	14.4.82	Mar-84	K Johns	Apr-82	N24/2	Manganese Point
17	GP	14.4.82	Mar-84	O Sutherland	7.4.82	N1& 2/2	Kapowairua
18	RR	14.4.82	Mar-84	O Sutherland	Apr-82	N14/1	Horeke
19	RR	14.4.82	Mar-84	O Sutherland	Apr-82	N1 &2/1	Te Ngako
20	RR	4.5.82	Mar-84	E D Hatch	1930-31	N41/1	Kaitarakihi
21	RR	23.5.82	Mar-84	P Matthews	16.5.82	N15/2	Pungatere Stream
22	RR	23.5.82	Mar-84	P Matthews	16.5.82	N15/3	Waikahikatea Stream
23	GP	23.5.82	Mar-84	P Matthews	16.5.82	N15/4	Ngawha Settlement
24	RR	23.5.82	Mar-84	P Matthews	17.5.82	N15/6	Kaikohe Museum
25	RR	23.5.82	Mar-84	P Matthews	17.5.82	N15/7	Whakatata Road
26	GP	23.5.82	Mar-84	P Matthews	17.5.82	N15/7	Whakatata Road
27	RR	23.5.82	Mar-84	P Matthews	17.5.82	N15/8	Okokako Road
28	RR	23.5.82	Mar-84	P Matthews	19.5.82	N15/9	—
29	GP	23.5.82	Mar-84	P Matthews	19.5.82	N15/10	Ridgens Road
30	GP	23.5.82	Mar-84	P Matthews	20.5.82	N11/2	Te Arakanihi
31	RR	23.5.82	Mar-84	P Matthews	20.5.82	N15/11	Pakaraka
32	RR	23.5.82	Mar-84	P Matthews	21.5.82	N23/1	Te Kawa Stream
33	Malahu	31.5.82	—	R Fullerton	Mar-82	—	Totokoitu Research Station, Rarotonga
34	Eddoe	1.6.82	—	P Brook	Jan-82	N24/2	Manganese Point
35	RR	2.6.82	Mar-84	P Matthews	21.5.82	N18 & 22/1	Waipoua Forest Headquarters
36	RR	8.6.82	Mar-84	E Cameron	7.6.82	N14/2	Matamata Stream
37	GR	22.6.82	Mar-84	M Bellingham	Jun-82	N14/7	West Coast Road
38	RR	30.8.82	Mar-84	A Wright	Aug-82	N8/7	Mahinepua
39	RR	8.9.82	Mar-84	W Booth	3.9.82	N11/7	Waiau Bay
40	?	15.9.82	—	E Cameron	15.8.82	—	Takuvaine Stream, Rarotonga
41	RR	16.9.82	Mar-84	M Heginbotham	Sep-82	N70/2	Opape
42	RR	22.10.82	Mar-84	K Jones	Oct-82	N78/2	Opotiki
43	RR	22.10.82	Mar-84	K Jones	Oct-82	—	Crarer Street, Wairoa
44	RR	10.11.82	Mar-84	P Whitehead	Feb-82	—	Coromandel Peninsula
45	RR	15.11.82	Mar-84	R Booth	Nov-82	N11/9	Te Tii
46	RR	6.12.82	Mar-84	P Matthews	30.11.82	N8/8	Papatara Bay
47	RR	6.12.82	Mar-84	P Matthews	1.12.82	—	Waiiti Bay
48	RR	6.12.82	Mar-84	P Matthews	1.12.82	N8/10	Waiiti Bay
49	RR	6.12.82	Mar-84	P Matthews	1.12.82	N8/11	Waiiti Bay
50	RR	6.12.82	—	P Matthews	1.12.82	N8/12	Kikipaku Stream

51	RR	6.12.82	Mar-84	P Matthews	3.12.82	N11/6	Howe Point
52	RR	6.12.82	Mar-84	P Matthews	3.12.82	N11/11	Waitata Bay
53	RR	10.1.83	Mar-84	P Matthews	30.12.82	N34/1	Swansea Bay
54	RR	10.1.83	Mar-84	P Matthews	30.12.82	N34/2	Swansea Bay
55	RR	10.1.83	Mar-84	P Matthews	1.1.83	NZMS259/6	Whangapoua Beach
56	RR	14.1.83	Mar-84	C West	Jan-83	N63/1	Onepoto Bay
57	RR	1.2.83	Mar-84	M Bellingham	Jan-83	N14/8	Wharekawa Road
58	RR	1.2.83	Mar-84	P Matthews	21.1.83	N61 & 60/1	Kopuni Point
59	RR	1.2.83	Mar-84	P Matthews	26.1.83	N80 & 81/1	Mangahauni Valley
60	RR	1.2.83	—	P Matthews	24.1.83	N72/5	Putanga Marae
61	GR	1.2.83	Mar-84	P Matthews	23.1.83	N63/4	Te Hekawa
62	RR	1.2.83	Mar-84	P Matthews	23.1.83	N63/3	Te Hekawa
63	GP	1.2.83	Mar-84	P Matthews	20.1.83	N70/4	Rerepa Stream
64	RR	1.2.83	Mar-84	P Matthews	21.1.83	N62/1	Taratua Point
65	RR	1.2.83	Mar-84	P Matthews	21.1.83	N61 & 60	Hamana Stream
66	RR	1.2.83	Mar-84	P Matthews	20.1.83	N70/3	Otehirinaki
67	GR	14.2.83	—	P Matthews	3.2.83	N14/12	Whirinaki
68	RR	14.2.83	Mar-84	P Matthews	3.2.83	N14/12	Whirinaki
69	GR	14.2.83	Mar-84	P Matthews	4.2.83	N18 & 22/2	Waimamaku Beach Rd.
70	RR	14.2.83	Mar-84	P Matthews	4.2.83	N18 &	Waimamaku Beach Rd.
71	GP	14.2.83	Mar-84	P Matthews	5.2.83	N14/14	Waiotemarama
72	GR	14.2.83	Mar-84	P Matthews	7.2.83	N10/4	Mangamuka
73	GR	14.2.83	—	P Matthews	8.2.83	N14/30	Reena
74	GP	14.2.83	—	P Matthews	8.2.83	N14/30	Reena
75	GP	14.2.83	Mar-84	P Matthews	9.2.83	N9 & 13/5	Ngair Stream
76	GP	14.2.83	Mar-84	P Matthews	10.2.83	N9 & 13/10	Tauroa Peninsula
77	RR	14.2.83	Mar-84	P Matthews	10.2.83	N10/12	Whangatane
78	GR	14.2.83	Mar-84	P Matthews	11.2.83	N10/1	Te Rore Stream
79	black	28.2.83	—	M Rau-Kupa	25.2.83	N109/1	Raleigh Street
80	?	13.4.83	—	G Fuller	13.4.83	N109/2	Pukekura Park
81	?	13.4.83	—	G Fuller	13.4.83	N109/2	Pukekura Park
82	?	13.4.83	—	G Fuller	13.4.83	N109/2	Pukekura Park
83	GR	27.4.83	Mar-84	J Coster	Apr-83	N3+4/1	Waihopo
84	RR	16.8.83	Mar-84	P Matthews	16.8.83	N35/1	Port Charles
85	GR	16.8.83	Mar-84	P Matthews	15.8.83	N39/4	Colville
86	RR	26.9.83	Mar-84	V Rickard	18.3.83	N37/5	Woodhill
87	sp?	15.1.84	—	P Matthews	11.2.83	N10/20	Bell's Hill

Appendix 4. Specimens of *Colocasia* in New Zealand herbaria

CHR = Botany Division, DSIR, Christchurch.

WELT = The National Museum,

AK = Auckland War Memorial Museum.

AKU = Department of Botany, University of Auckland.

Other herbaria were not checked.

Herbarium	Number	Collector	Coll. date	Location	Description
CHR	None in collection		—	(E Godley, pers. comm. 1981)	
WELT	?	Rev. E Jennings	29.5.1897	?	' <i>Taro hohia</i> '
WELT	?	G Abercrombie	pre 1897	Kioreroa, Whangarei	?
WELT	?	N M Adams	23.3.1979	Manganese Point, Whangarei	?
AK	477	T F Cheeseman	Feb 1895	Waimate, Bay of Islands	flower
AK	5476	R H Matthews	Apr-21	Kaitaia	flower
AK	44326	R C Cooper	Jun-56	Met. Station, Raoul Island	flower
AK	70451	A T Pycroft	Apr-62	Auckland	flower
AK	71737	R C Cooper	?	St. Heliers, Auckland	flower
AK	90327	A Leahy	Dec-63	Kerikeri	flower
AK	90328	A Leahy	Dec-63	Kerikeri	flower
AK	90329	A Leahy	Dec-63	Kerikeri	flower
AK	90330	A Leahy	Dec-63	Kerikeri	flower
AK	95475	M Hodgkins	Nov-45	Tauranga	leaf
AK	123004	D Simmons	May-70	Remuera, Auckland	flower
AK	151544	D Simmons	Feb-74	Remuera, Auckland	flower
AK	151597	D Simmons	Apr-80	Remuera, Auckland	flower
AKU	14354	P Matthews	8.2.1983	North Hokianga	flower, variant GP
AKU	14693	P Matthews	18.3.1983	ex Site N109/1 (New Plymouth)	leaf, AKL 79
AKU	14694	P Matthews	18.3.1983	Botany Dept	leaf, variant RR, AKL62
AKU	14695	P Matthews	18.3.1983	Botany Dept	leaf, variant RR, AKL2
AKU	14696	P Matthews	18.3.1983	Botany Dept	leaf, variant GR, AKL37
AKU	14697	P Matthews	18.3.1983	Botany Dept	leaf, variant GP, AKL29
AKU	14699	P Matthews	18.3.1983	Botany Dept	leaf, AKL34
AKU	14832	P Matthews	12.4.1983	Botany Dept	flower, AKL80
AKU	15137	P Matthews	17.1.1984	Botany Dept	leaf, flag leaf, AKL81
AKU	15138	P Matthews	17.1.1984	Botany Dept	leaf, AKL82
AKU	15139	P Matthews	17.1.1984	Botany Dept	leaf, AKL87

Appendix 5. Leaf sample sites and descriptions

Leaf sample descriptions for taro variants RR, GR, and GP, showing site number, location, date, site category (garden/wild), and site description. Descriptive statistics are given for the largest measured blade dimension, A, the front lobe, to indicate variation in size within and between sites. Site categories are defined in Chapter Seven. 'Stream' implies flowing water at time of observation, unless otherwise indicated.

	n	mean cm	s.d. cm	min. cm	max. cm	covariance %
VARIANT RR						
N8/8	Papatarā Bay, Cavalli Islands; 30.11.82; wild; in streams, clumps scattered along streams.					
	12	18.8	6.0	10.3	26.7	32
N8/13	Rere Bay, Whangaroa; 2.12.82;?; plants on flat beside stream.					
	1	17.7	-	-	-	-
N10/12	Awanui Flat, Kaitaia; 10.2.83; wild; clay topsoil clumps under light scrub near a stream.					
	12	18.2	5.4	10.4	26.2	30
N14/12	Whirinaki, Hokianga; 3.2.83; garden, non-cultivated, non-derelict; clumps growing in boggy ditch above river, mixed with clumps of variant GR.					
	12	20.1	7.9	7.1	30.6	39
N15/3	Waikahikatea Stream, Bay of Islands; 16.5.82; wild; clumps scattered in and beside stream, by pasture.					
	12	23.8	12.6	5.7	45.0	52
N15/8	Okokako Road, Bay of Islands; 17.5.82; wild; taro in stream flowing through pasture and bush and into swampy flats (the fanner reports a big patch of taro was washed out twelve months ago).					
	2	27.8	3.9	25.0	30.5	15
N15/11	Waikopiro Stream, Bay of Islands; 20.5.82; garden, non-cultivated. non-derelict; single clump amongst large patch of Canna in boggy bank beside stream.					
	3	2.1	12.8	24.4	46.8	40
N18/2	Waimamaku Road, Hokianga; 4.2.83; garden, non-cultivated, non-derelict; variants RR and GR in mixed and separate clumps, scattered along dry stream bed through pasture.					
	11	20.1	5.2	13.2	28.5	26
N23/4	Te Kawa Stream, Dargaville; 21.5.82; garden, cultivated; in shade - measured seven shade leaves; also measured twelve leaves from single wild clump upstream, in clay topsoil, in open pasture (recorded as Site N23/1).					
	19	20.2	19.8	4.8	56.0	98
NZMS259/6	Whangapoua Beach, Great Barrier Island; 1.1.83; wild; clumps in patch in flat pasture beside creek.					
	12	24.2	11.7	11.5	49.0	48
N42/4	Mt. Albert, Auckland; 24.4.82; garden, cultivated; fertile volcanic soil, single clump.					
	44	22.2	13.5	3.4	46.0	61
N43/7	Coromandel Peninsula; 14.8.83; wild; clumps along narrow stream at mouth of steep-sided coastal gully, leaves weather-damaged.					
	12	19.1	4.5	12.0	24.5	24

N70/2	Ohope, East Cape; 19.1.83; garden, non-cultivated, non-derelict; clumps in patch at site of former garden, in wet pasture at foot of a slope.					
	12	18.0	6.0	8.2	27.5	33
N80/1	Mangahauni Valley, East Cape; 26.1.83; garden, non-cultivated, derelict; clumps dispersed over open pasture in fan where streamlet emerges from gully, plants originate from clumps in stream beside house, on hill above.					
	12	18.1	5.4	11.3	30.2	30
VARIANT GR						
N10/1	Te Rore Stream, Kaitaia; 11.2.83; wild; clumps scattered along stream and stream banks.					
	12	31.0	11.5	14.8	44.0	37
N14/12	Whirinaki, Hokianga; 3.2.83; garden, non-cultivated, non-derelict; clumps growing in boggy ditch above river, mixed with clumps of variant RR.					
	12	28.5	11.0	15.5	46.2	39
N14/30	Reena, Hokianga; 8.2.83; wild; two clumps in drier upper part of stream at edge of forest and pasture, above a very large patch of variant GP.					
	11	24.1	9.1	13.7	43.0	38
N18/2	Waimamaku Road, Hokianga; 4.2.83; garden, non-cultivated, non-derelict; variants GR and RR in mixed and separate clumps, scattered along dry stream bed through pasture.					
	12	21.0	7.9	11.9	36.0	37
N39/6	Curtis farm, Coromandel Peninsula; 15.8.83; garden, non-cultivated, non-derelict; clumps in boggy soil and humus near streamlet under forest, mixed with variant RR.					
	12	15.4	5.0	7.0	24.5	33
N63/4	Te Hekawa, East Cape; 23.1.83; garden, non-cultivated, non-derelict; in streamlet above coastal road.					
	12	24.3	8.8	12.2	38.5	36
VARIANT GP						
N11/2	Te Arakanihi, Bay of Islands; 20.5.82; wild; clumps scattered over damp ground in weedy area by swamp, amongst light scrub.					
	12	29.2	9.1	18.4	46.5	31
N14/3	Mitimiti Road, Hokianga; 8.2.83; garden, non-cultivated, derelict; plants in clay soil in damp roadside ditch, by pasture, down-slope from stunted clumps in dry ground before derelict house.					
	12	21.3	5.7	9.8	29.0	32
N14/14	Waiotemarama, Hokianga; 5.2.83; garden, non-cultivated, non-derelict; clumps in boggy stream bed, growing with broad shade leaves and bronze colouring on petioles, under trees.					
	12	27.9	8.4	17.0	41.8	30
N14/30	Reena, Hokianga; 8.2.83; wild; dense patch of clumps in large area of boggy ground by pasture.					
	12	24.8	9.8	11.0	43.0	39
N15/4	Ngawha, Bay of Islands; 16.5.82; wild; dense patch of clumps in large area of boggy ground by pasture.					
	24	22.7	10.0	7.4	43.4	44
N15/12	Kawakawa - Paihia Road; 20.5.82; wild; clumps dispersed along stream and stream banks, by pasture.					
	12	27.7	14.1	9.4	51.0	51
N70/4	Rerepa Stream, East Cape; 20.1.83; wild; clumps dispersed over long distance of stream amongst weeds, boggy ground.					
	12	28.0	12.8	10.8	46.5	46

Appendix 6. Leaf morphology

Ap. 6.1 Example data recording sheet

Measurements of the length of corm between the petiole base and the ground (bg) were not made. Petiole lengths were measured from the tip to the base of the petiole (pb) where possible, or from the tip to the ground surface (pg) otherwise.

DATE		26-1-83		LOC	Manghauwi	SITE	N80+61/1		COLL.	AKL 59, RR		PAGE	10	
SHOOT NO.	LEAF NO.	PETIOLES			A	B	C	D	E	F	G	COMMENTS		
		bg	pb	pg										
1	1		59		24.4	12.6	12.4	7.0	13.4	12.4	9.5			
	2		68		30.2	14.1	14.3	8.2	14.7	12.6	11.0			
	3		52		20.5	10.4	10.0	6.2	9.6	9.0	8.5			
2	1		52		19.2	11.8	12.2	6.6	10.5	11.3	8.0	has spider nettes		

Ap. 6.2 Univariate descriptive statistics

(a) Observed leaf characters. Units in centimetres except for skewness (unitless).

	Variant RR					Variant GR					Variant GP				
	n=176					n=71					n=96				
	\bar{x}	s.d.	skew	min.	max.	\bar{x}	s.d.	skew	mm.	max.	\bar{x}	s.d.	skew	mm.	max.
(a) Observed Character															
A	20.9	11.3	0.79	3.4	56.0	24.0	10.2	0.8	7.0	46.2	25.5	10.3	0.39	7.4	51
B	12.1	6.5	0.63	0.5	32.5	12.9	4.9	0.58	3.4	24.5	16.8	6.8	0.32	3.5	32.2
C	12.0	6.6	0.71	0.3	34.5	12.6	4.8	0.53	3.8	23.8	16.6	6.8	0.33	4.1	32.0
D	6.7	3.8	0.79	0.1	19.5	7.3	3.4	1.60	2.0	22.5	6.6	3.1	0.56	1.4	14.1
E	11.1	5.9	0.68	1.4	28.5	12.0	4.7	0.63	3.5	25.0	12.9	5.5	0.45	3.0	25.0
F	11.5	6.2	0.82	1.2	31.5	12.1	4.3	0.49	3.8	22.2	13.2	5.6	0.34	3.4	26.3
G	8.9	4.8	0.75	0.7	25.0	10.5	4.6	0.61	1.8	23.0	16.8	7.6	0.60	4.0	36.0
petiole height	58	25	—	7.5	119	65	25	—	18.5	132	78	34	—	18.0	175

(b) Derived characters. The derived characters are calculated as follows:

$$\text{sinus angle (degrees)} = 2 \cdot \sin^{-1} (G/B+C)$$

$$\text{symmetry} = (E \times B)/(F \times C)$$

$$\text{lobedness} = (B+C)/2/A$$

$$\text{peltateness} = D/A$$

$$\text{width/length} = (E+F) / A$$

$$\text{rear/width} = G/(E+F)$$

	Variant RR					Variant GR					Variant GP				
	n=176					n=71					n=96				
	\bar{x}	s.d.	skew	min.	max.	\bar{x}	s.d.	skew	mm.	max.	\bar{x}	s.d.	skew	mm.	max.
(b) Derived character															
sinus angle	46.8	9.4	3.52	27,8	122.1	47.8	8.2	-0.17	26.6	67.7	60.2	10.8	-0.02	28.1	86.7
symmetry	1.00	0.18	0.91	0,35	1.94	1.02	0.14	1.10	0.81	1.47	1.00	0.13	0.18	0.44	1.59
lobedness	0.58	0.11	1.26	0.12	1.37	0.54	0.08	-0.80	0.26	0.70	0.66	0.08	2.26	0.51	1.08
peltateness	0.32	0.07	1.37	0.03	0.72	0.31	0.06	1.00	0.17	0.52	0.25	0.04	0.9	0.16	0.44
width/length	1.10	0.17	3.04	0.68	2.47	1.03	0.15	-0.76	0.5	1.36	1.02	0.11	1.54	0.65	1.64
rear/width	0.40	0.07	0.52	0.20	0.70	0.43	0.07	-0.22	0.25	0.61	0.64	0.11	0.52	0.31	1.10

Appendix 7. *Aweu*, a wild taro in Hawai'i

Description of the Hawai'ian taro variety *Aweu* (Whitney et al. 1939). This variety resembles the New Zealand taro variant GP in morphology (Chapter Five) in its occurrence in the wild, and possibly also in its poor eating quality (Chapter Seven). Whitney et al. (1939) describe two types in the category of rhizome (stolon) producing varieties, but regards these as unrelated. They are noted as commercially the least important of all the taros, since the rhizomes increase the difficulty of cultivation and harvesting. The *piko* is the upper surface of the blade above the point of petiole insertion.

Variety (Number and Name): 6. *Aweu*. Other Names: *Aweo*, *Aweoweo*, *Aweuweu*, *Mamauweo*, *Maauweo*.

General Characteristics: Medium in height to tall. Moderately spreading, maturing within 9 to 12 months, producing from 10 to 15 long slender rhizomes, distinguished by length of rhizomes. Petiole: 70 to 105 cm long, light green often inconspicuously flecked with dark green near base, white at base, with narrow, light purplish to indistinct edge, curved sharply at apex so that blade hangs vertically. Leaf Blade: 40 to 65 cm long, 25 to 45 cm wide, 35 to 55 cm from tip to base of sinus, narrowly ovate, thin in texture, light green, margins slightly undulate, *piko* greenish to faintly purple, lobes acute with shallow, narrow sinus. Corm: Flesh white with yellowish fibres; skin cream-coloured, usually with pink or purple along leaf-scar rings, the outer skin shaggy and fibrous. Origin and derivation of Name: Native variety; derives its name from shaggy outer skin of corm. Distribution: Formerly widely distributed in wild state, now scattered along streams and

in forests in the mountains. Use: Good as *poi*, but not used at present because the corras are usually small; the leaves are used for *luau*. Remarks: This variety was used by the old Hawai'ians for *poi* only when other food was scarce. The corms are too acrid to be used as table taro unless cooked for a long time. *Aweu* is often called wild taro because of its frequent occurrence in the wild state. The rhizomes, sometimes as long as 70 cm, come so close to the surface that they appear like creeping stolons.

Appendix 8. Flowering in New Zealand and Hawai'i

Ap. 8.1 Observations by P. J. Matthews, 1982–83

Each taro inflorescence is identified by either its number in the sequence recorded, or by its number in the sequence of inflorescences produced by the shoot. The *flower reference number* is given for cross-reference to the records of flowering (Table 5.1).

The developmental stage of each inflorescence is identified by the state of the upper spathe, as follows, (younger to older): G = green. G, Y = green and yellow together. Y = yellow. Y, O = yellow and orange together. O = orange. O, B = orange and brown together. B = brown. Wi = withered. pe = pre-emergent. Note: measurements for one flower (first in table) on two dates are given to illustrate shrinkage of the upper spathe during maturation.

Variant/ALK No.	Flower ref. no.	Shoot number	Infl. number	Infl. position	Date	Spathe (cm)			Spadix (cm)				Ratio				
						Stage	Total length	Lower part	Upper part	Total length	Pistillate zone	Sterile mid-zone	Staminate zone	Sterile appendage	Spat.		
															Lower/Upper	Sterile Ap./Spadix	Sterile Ap./Stam. Z.
RR	1	1	1	1	9.3.82	Y	28.2	5.2	23						0.23		
					11.3.82	O,B	25.5	5.5	20			2.0	6.1	4.3	0.28		0.70
				2	10.3.82	Y	26.5	5.5	21						0.26		
				5	17.3.82	pe				10.8	2.0	1.4	4.2	3.2		0.30	0.76
		2		1	19.3.82	Y	23.5	4.5	19						0.24		
RR	2	1		1	25.3.82	G,Y	20	4.2	15.8						0.21		
RR	3			1	15.7.82	G	30	6.0	24.0	18.8	3.6	2.8	7.5	4.9	0.20	0.26	0.65
RR	4	1		2	12.3.83	Wi				10.3	2.2	1.4	4.8	1.9		0.18	0.40
				4	12.3.83	Y				12.0	3.0	1.5	5.5	2.0		0.17	0.36
RR	5		1	?	15.7.83	Y				15.8	4.3	1.8	5.8	3.9		0.25	0.67
GP	6	1		2	8.2.83	Y				8.8	2.3	1.6	2.3	2.6		0.30	1.13
		3		1	8.2.83	W				8.8	4.6	0	2.5	1.7		0.19	0.68
		4		1	8.2.83	W				9.0	4.2	0	3.1	1.7		0.19	0.55
GP	6	4		2	8.2.83	Wi				11.4	3.6	1.3	3.7	2.8		0.25	0.76
GP	7	1	1	?	8.2.83	Y				10.2	3.5	2.3	1.8	2.6		0.25	1.44
		2	1	?	8.2.83	Y				10.0	3.3	1.9	2.0	2.8		0.28	1.40

		3	1	?	8.2.83	Y				12.1	3.7	1.8	3.7	2.9		0.24	0.78
		4	1	?	8.2.83	Y				10.1	3.5	1.7	2.4	2.5		0.25	1.04
		5	1	?	8.2.83	Y				11.1	3.5	2.3	2.5	2.8		0.25	1.12
		6	1	?	8.2.83	Y				8.6	3.0	1.6	2.2	1.8		0.21	0.82
GP		7	1	?	8.2.83	Y				12.2	4.0	1.8	3.2	3.2		0.26	1.00
		8	1	?	8.2.83	Y				10.5	3.6	2.4	2.0	2.5		0.24	1.25
		9	1	?	8.2.83	Y				13.1	4.7	2.4	2.8	3.2		0.24	1.14
GP	8	1	1	?	9.2.83	Y				11.2	4.2	1.7	3.0	2.3		0.21	0.77
		2	1	?	9.2.83	Y				12.8	4.0	2.0	3.5	3.3		0.26	0.94
		3	1	?	9.2.83	Y				11.5	3.5	2.0	3.2	2.8		0.24	0.88
GP	9	1	1	?	9.2.83	Y				12.4	3.5	2.5	3.8	2.6		0.21	0.68
GP	9	2	1	?	9.2.83	Y				13.2	4.4	2.0	3.5	3.3		0.25	0.94
		3	1	?	9.2.83	Y				12.5	3.9	1.6	3.8	3.2		0.26	0.84
		4	1	?	9.2.83	Y				9.1	3.0	2	2.0	2.1		0.23	1.05
		5	1	?	9.2.83	Y				10.9	3.5	1.6	3.0	2.8		0.26	0.93
80	10	1	1		12.4.83	Y				16.0	7.2	2.0	2.3	4.5		0.28	2.00
80	11	1		?	Sep-83	B				13.5	3.5	3.0	3.3	3.7		0.27	1.12
12	12	1	1	?	29.4.83	Y	22.4	3.8	18.6	8.4	2.2	1.6	3.5	1.1	0.20	0.13	0.31
1	13	1	1	?	29.4.83	Y	14.6	3.3	11.3	6.0	1.5	1.6	2.4	0.5	0.29	0.08	0.21
16	14	1	1	?	25.4.83	Y	18.2	3.5	14.7	6.7	1.5	1.5	3.0	0.7	0.24	0.10	0.23

Ap. 8.2 Observations by R C Cooper (1969)

The taro variety identifications are those made by E C Cooper. The ratios are calculated here from the previously published measurements.

Cheeseman Herbarium Specimen Number	Variety	Location	Date	Spathe (cm)	Spadix (cm)						Ratios		
				Total Length	Total Length	Pistillate Zone	Sterile Mid-zone	Staminate Zone	Sterile Appendage	Sterile Append. Spadix	Sterile Append. Staminate		
477	?	Waimate	Feb 1895	15.5									
5476	antiquorum	Kaitaia	Apr 1921	22.5	14.9	3.1	2.3	4.9	4.6	0.31	0.94		
44326	esculenta	Lava Pt.	June 1956	16.4	6.0	1.8	1.2	2.5	0.5	0.08	0.20		
70451	esculenta	Edmund St.	Apr 1962	26.6	13.8	3.0	2.0	6.5	2.3	0.17	0.35		
90327	esculenta	Ngairi Bay	Dec 1963	24.1	9.1	1.9	2.5	2.4	2.3	0.25	0.96		
90328	esculenta	Kerikeri bch	Dec 1963	22.8	9.2	5.5		1.7	2.0	0.22	1.18		
90329	esculenta	Kerikeri bch	Dec 1963	26.2	8.7	5.6		2.5	0.6	0.07	0.24		
90330	esculenta	Kerikeri bch	Dec 1963	25.6	8.7	5.5		2.6	0.6	0.07	0.23		
118571	antiquorum	Whareora	Sept 1968	18.1	11.8	3.8	1.1	3.7	3.2	0.27	0.86		

Ap. 8.3 Observations by Whitney et al. (1939) on a field-station varietal collection

These authors present only range end-point values. Range mid-point values have been calculated here for the estimation of the ratios. The variety numbers are those given by Whitney et al. (1939). A large majority of the varieties listed here were collected within the Hawai'ian Islands.

GROUP	VARIETY		SPATHE (cm)					SPADIX (cm)				RATIOS	
			Total Length		Lower Part		Upper Part	Total Length		Sterile	Append.	Spathe	Spadix
	No.	Name	Range	Mid-point	Range	Mid-point		Range	Mid-point	Range	Mid-point	Lower Upper	Sterile Append. Spadix
Rhizomatous	7	<i>Kakakura-ula</i>	24-32	28	4-5	4.5	23.5	9-11	10	0.7-1.3	1	0.19	0.1
Mana	11	<i>Mana Uliuli</i>	12-16	14	2-2.5	2.25	11.75	6-9	7.5	0.4-0.8	0.6	0.19	0.08
	12	<i>Mana Ulaula</i>	14-17	15.5		3	12.5	4-5	4.5	0.5-0.6	0.55	0.24	0.12
	15	<i>Mana Kukuluhema</i>	21-24	22.5	3-4	3.5	19	7-8	7.5	0.4-0.5	0.45	0.18	0.06
Piko	18	<i>Piko Kea</i>	15-20	17.5	3-4.5	3.75	13.75	5-6	5.5		0.4	0.27	0.07
	21	<i>Piko Uliuli</i>	15-20	17.5	3-4.5	3.75	13.75	5-6	5.5		0.4	0.27	0.07
	22	<i>Piko Eleele</i>	15-20	17.5	3-4.5	3.75	13.75	5-6	5.5		0.4	0.27	0.07
	23	<i>Elepaio</i>	17.5-18	17.75		2.5	15.25		6	0.7-0.8	0.75	0.16	0.13
	24	<i>Uahiapele</i>	18-24	21	3-4	3.5	17.5		6		0.6	0.20	0.10
	26	<i>Tahitian</i>		30		5	25					0.20	
Kai	27	<i>Kai Uliuli</i>	18-20	19		4	15	7-8	7.5		0.4	0.27	0.05
	28	<i>Kai Ala</i>	19-22	20.5	3-4	3.5	17	7-9	8	0.7-1.0	0.85	0.21	0.11
	29	<i>Kai Kea</i>	18-23	20.5	3-4	3.5	17	6-9	7.5	0.7-1.1	0.9	0.21	0.12
	30	<i>Apuwai</i>					20-25	17-20	18.5		1		0.05
	32	<i>Piialii</i>	26-33	29.5	4.5-9	6.75	22.75	9-12	10.5	1.2-2	1.6	0.30	0.15
	33	<i>Paakai</i>	21-24	22.5	3-4	3.5	19	7-8	7.5	0.8-0.9	0.85	0.18	0.11
	34	<i>Moana</i>	22-25	23.5	4-5	4.5	19					0.24	
	35	<i>Akuugawai</i>	26-28	27	1-4.5	4.25	22.75	8.5-9	8.75		1	0.19	0.11
Lauloa	36	<i>Lauloa Eleele-omao</i>	30-35	32.5	5.5-6	5.75	26.75					0.21	
	38	<i>Lauloa PaUakea-eleele</i>	32-37	34.5	5-6	5.5	29		11		1.3	0.19	0.12
	40	<i>LauZoa Palakea-papamu</i>	20-24	22		4	18	8-10	9		1.1	0.22	0.12
	41	<i>Lauloa Palakea-keokeo</i>	30-35	32.5	5.5-6	5.75	26.75		12	1.2-1.7	1.45	0.21	0.12
Eleele	43	<i>Eleele Makoko</i>	22-25	23.5	3.5-4.5	4	19.5	7-9	8	0.6-0.7	0.65	0.21	0.08
	44	<i>Eleele Naioea</i>	24-26	25	3.5-4.5	4	21	8-9	8.5	0.6-0.7	0.65	0.19	0.08
	45	<i>Marnini-owali</i>	26-30	28	4.5-5.5	5	23	10-11	10.5	1.1-1.2	1.15	0.22	0.11
	47	<i>Nawao</i>	18-23	20.5	3-4	3.5	17					0.21	
Ulaula	48	<i>Ulaula Kumu</i>	21-23	22	3-4	3.5	18.5		7	0.4-0.5	0.45	0.19	0.06
	55	<i>Manini Toreto</i>		28					9		0.8		0.09
	59	<i>Manini-opelu</i>	28-32	30	4-5	4.5	25.5					0.18	
	60	<i>Hinupuaa</i>		24	4-5	4.5	19.5		8		0.7	0.23	0.09
Lehua	63	<i>Lehua Maoli</i>	14-20	17	2.5-3	2.75	14.25	6-7	6.5	0.6-0.8	0.7	0.19	0.11
	66	<i>Lehua palaii</i>	18-23	20.5	3-4	3.5	17	7-8	7.5	0.5-0.8	0.65	0.21	0.09
	68	<i>Wehiwa</i>	22-26	24	3-3.5	3.25	20.75		10	0.8-0.9	0.85	0.16	0.09
	71	<i>Leo</i>	15-17	16	2.5-3	2.75	13.25	6-7	6.5	0.8-1.1	0.95	0.21	0.15
	73	<i>Haokea</i>	26-37	31.5	4-5	4.5	27	8-11	9.5	0.9-1.4	1.15	0.17	0.12
Unclassified	83	<i>Pikoele</i>	18-20	19		3	16	6.5-7	6.75		0.9	0.19	0.13

Appendix 9. Māori naming of taro

Introduction

During the present study, a small amount of information was obtained on the Māori naming of taro. The records listed below and the following discussion are intended simply as a starting point for anyone who wishes to take the topic further.

List of names and sources

Many of the names listed here come from the list of 45 names collated by Best (1976) from the nineteenth century records of W. Colenso, J. White, E. Tregear (1891) and the *Williams' Māori Dictionary* (edition not specified). Where authors are referred to without a publication year, the listed name has been only sighted in Best (1976). Names reported by correspondents (see Appendix 1) are indicated as personal communications. Names encountered during fieldwork, 1982–83, are indicated by the author's name (P. J. Matthews) followed by the date of the field notes (also held at the Herbarium).

Except for two names known to be derived from overseas place names, no capitals have been used, though this may not be strictly correct and does not always follow the reports; however, reports also vary. Names applied to or implying introductions after European arrival are listed separately at the end.

NAME	SOURCES
awhanga	V. Gregory, pers. comm. 1983
awanga	Colenso 1880; White
hanina	V. Gregory, pers. comm. 1983
haukopa	Colenso 1880; Biggs 1981
ipurangi	Taylor 1848; Tregear
taro ipurangi	V. Gregory, pers. comm. 1983
kakaratapae	V. Gregory, pers. comm. 1983
kakatarahaere	Williams
kakatarahae	Colenso 1880
kakatupari	Taylor 1848; Tregear
kaokao-paraoa	White
kauere	Biggs 1981
kaunaunga	Taylor 1848; Tregear
keakea	Taylor 1848; Tregear
kiekie	White
kinakina	Colenso 1880; White; Biggs 1981
koareare	Colenso 1880; V. Gregory, pers. comm. 1983
kohuarangi	Colenso; Williams
kohuhurangi	Biggs 1981
kohukohurangi	Biggs 1981

kohuorangi	Colenso 1880; White; Biggs 1981
kohurangi	Williams; V. Gregory, pers. comm, 1983
kokohurangi	Biggs 1981
maehe	Taylor 1848; Tregear
maire	White
makati	V. Gregory, pers. comm. 1983
makatiti	Williams; D. Yen, pers. comm. 1983; A. Sheward, pers. comm. 1984
matatiti	Colenso 1880
mamaku	Colenso 1880; V. Gregory, pers. comm. 1983
manuwenua	Taylor 1848; Tregear
taro maori	Wilson 1894; K. Reynolds, pers. comm. 1982; V. Gregory, pers. comm. 1983; P.J. Matthews 17.5.82, 19.1.83.
real Māori taro	P. J. Matthews 19.5.82, 5.2.83, 8.2.83
old Māori taro	P. J. Matthews 4.2.83
ngaue	Williams
ngaau	Biggs 1981
ngongoro	Colenso 1880
patai	Colenso 1880
paatai	Biggs 1981
paeangaanga	Colenso 1880; Williams; White; V. Gregory, pers. comm. 1983
pehu	Williams; Biggs 1981
pakaue	Williams; Biggs 1981
pongi	Taylor 1848; Williams; White; V. Gregory, pers. comm. 1983
pongi matapo	Best 1976
pongo	Colenso 1880
pongu	D. E. Yen, pers. comm. 1983
taro punga	A. Sheward, pers. comm. 1984
poporo	Gregory, pers. comm. 1983
potango	Colenso 1880; White; P. J. Matthews 19.5.82
potangotango	V. Gregory, pers. comm. 1983
takatakapo	V. Gregory, pers. comm. 1983
takatakaapo	Colenso 1880
tanae	Williams; Biggs 1981
tangae	Taylor 1848; Tregear
taropo	White
tautaumahi	V. Gregory, pers. comm. 1983
tataumahei	Colenso 1880
tokotokohau	Colenso 1880; Biggs 1981
turitaka	Colenso 1880; White; Biggs 1981
uhikoko	Colenso 1880
uhi (uwahi) koko	Biggs 1981

uhiraurenga	Colenso 1880
uhi (uwhi) raurenga	Biggs 1981
upokotike	V. Gregory, pers. comm. 1981
upokotiketike	Colenso 1880
taro upokotiketike	Sheward, pers. comm. 1984
wairuaarangi	Colenso 1880
wakahekerangi	Taylor 1848; Tregear
wakarewa	Taylor 1848; Tregear
akarewa	Williams; V. Gregory, pers. comm. 1983
taro akarewa	A. Sheward, pers. comm. 1984
whakatauare	Biggs 1981
Names applied to or implying introduction after European arrival:-	
taro hoia	Colenso 1880; Williams; D. Vincent, pers. comm. 1982; V. Gregory, pers. comm. 1983; I. Barber, pers. comm. 1983; B. Biggs, pers. comm. 1983; P. Tangiwai, pers. comm. 1983; A. Sheward, pers. comm. 1984; P. J. Matthews, 19.1.83, 25.1.83, 4.2.83, 5.2.83 (two occurrences), 7.2.83.
taro oia	Polack 1838
taro Merekena	Wilson 1894
taro poaka	P. J. Matthews 18.5.82
taro Tonga	P. Tangiwai, pers. comm. 1983

Discussion

Generally descriptions of the plants to which names apply are lacking. Colenso (1880) provides extremely cursory descriptions of varieties and only general statements regarding their location. The fullest descriptions have been provided by V. Gregory (pers. comm. 1983) but other correspondents give information also. An attempt was made (see correspondence to B. Biggs, pers. comm. 1983) to group Viv Gregory's descriptions according to the variant (RR, GR, or GP) which they most clearly resemble. This attempt has been abandoned because it requires the assumption that past and present Māori naming is based on only the three major variants recognised during the recent fieldwork.

Two other variants, as yet known from only single sources, have been claimed as historically associated with the Māori: AKL 34 was named as 'genuine' *taro maori* when presented at Pakaraka, Central Bay of Islands (K. Reynolds, hearsay only, pers. comm. 1982), and AKL 79, although named as 'black taro', for want of a better name, is regarded as a Māori taro and 'very old', (M. Rau-Kupa, pers. comm. 1983). These claims are indicative, but by no means substantiate, that a wider range of botanically distinct variants are historically important.

Recognition of the three variants, RR, GR, and GP, can be made using just two characters, namely blade shape and petiole colour. These characters appear stable, being more or less distinctive of each variant regardless of habitat. Their use reflects the belief that stable phenotypic characters distinguish the underlying genotype best. Such an understanding may not be explicit in taxonomies not of the European tradition. It is

characteristic of the folk-taxonomies of cultivated plants that varieties are distinguished on a great wealth of plant detail, including size, taste, internal texture and colour, as well as external shape and colour (Whitney et al. 1939; Panoff 1972; Bulmer 1974). Variations in such vegetative characters reflect to greater or lesser extents diversity in natural and cultivated habitats rather than genetic diversity. While the descriptions provided by V. Gregory (pers. comm. 1983) include such a wealth of plant detail, it is not known how much they actually reflect the original derivation of the names. A possible original derivation can be seen in the name *kakatarahae*, which means the ‘quarrelling or scratching parrots’ and may recognise astringency in the taro flesh (B. Biggs, pers. comm. 1983).

External associations, both cultural and physical, which might also be recognised in Māori naming include habitat type, place or area name, and personal or geographic sources. Although the descriptions made by V. Gregory (pers. comm. 1983) include many details of habitat which vary from variety to variety, it is not known how much these external details provide essential definition rather than coming after definition. External associations are clearly recognised, for example, in the names *taro maori*, *taro poaka* (taro fed to pigs), *taro Tonga*, and *taro Merekena* (American taro).

To what extent external associations are recognised in the other possibly more traditional names listed has not been established. There do appear to be at least two examples:

(1) *ngaue* is noted by R. McConnell (pers. comm.) as a suffix meaning ‘wet taro cultivation’ in a local East Cape stream name, Waingae;

(2) *ipurangi* is described by Best (1976) as a shallow type of *parua*, a basin-like hole in which taro is planted.

These examples however must be accepted with caution, since it is quite possible that the words in fact represent part of the vocabulary of cultivation, closely linked to the plants without actually naming them. The general lack of records of use in living context — i.e., ethnographic description — presents another stumbling block to interpretation of the listed names: the taxonomic positions of the names are not known, whether non-terminal (subdividable) or terminal (non-subdividable). For taro at least, the lower order groupings or structure of the Māori classification system has not been recorded. *Taro* clearly holds a non-terminal position in binomials such as *taro ipurangi*, while names such as *kakatarahae* and *kakatupari* could either be terminal uninomials or binomials with *kaka* representing a group of varieties. What proportion of the name list comprises of terminal taxa is unknown.

Bulmer (1970) comments on the question of correspondence between the terminal folk taxa of folk-taxonomies and the biological species recognised by the biologists of Western science. In particular he notes that vegetatively propagated domesticated plant species often include a host of genetically distinct varieties, with reasonably stable morphological characters, which maintain their identity by the fact of their vegetative propagation. It is then argued that the relatively large number of terminal taxa recorded for such cultivated plants reflects not ‘high cultural significance’ (i.e., external, cultural reasons for differentiating between plants) but objective observation of morphologically

and genetically distinct strains.

To some extent this argument may be correct, but only so far as Western science does in fact recognise genetic differences rather than simply differentiating between phenotypes for external, cultural reasons. This is well illustrated in the botanical classification of Hawai'ian taro cultivars by Whitney et al. (1939), who note that the vegetative characters which they use as criteria often group varieties which have little else in common. The correspondence between their classification and the traditional Hawai'ian naming is so great that many of the Hawai'ian group and variety names are retained, but this does not imply that the Hawai'ian system is based on objective observation of genetically distinct strains.

Objective observations are indeed made in the above examples, but classifications based on phenotypic characters cannot be guaranteed to reflect genetic differences well, regardless of any theoretical knowledge of the genetic basis of life. Direct knowledge of both genetic differentiation and reproductive barriers, (two criteria for identifying phylogenetic relationships or biological species), is extremely limited for taro (see Chapters Two and Three). Identification of formal sub-specific categories among the New Zealand taro has been expressly avoided for this reason, while the use of a species name (as in *C. esculenta*) has been simply for the sake of convention and convenience. The morphological distinctions between variants do suggest genetic differences, but are insufficient as criteria for defining biological species.

To summarise, evaluation of the correspondence of other folk-taxonomies with genetic differences, biological species, or other discontinuities in the biological world is limited by how well the evaluator's own folk-taxonomy does the same job.

Returning to the list of Māori names for taro, further issues regarding interpretation should be noted: transfer of names from one cultivar to another within a genus or between genera may occur (H. Leach, pers. comm. 1984); the list may combine names from different dialects; and the lost cultural and economic importance of taro has probably had important effects on error and consistency in both recorded and continuing usage.

This discussion began with the question of how many botanically distinct variants of taro are represented in the list of Māori names. Because of the problems outlined above it is clear that speculation would be of little value. A second question is now posed: What can be learnt about plant origins from the names?

Only a few names for taro were encountered during fieldwork, and more in correspondence. A general impression, by no means clear, has been obtained of some consistency in the present use of names with the use claimed in earlier records. Taro — which is thought of as belonging to the Māori, as historically important, as cultivated, and as that which is best for eating — may be named as *taro maori* or referred to in phrases such as 'real Māori taro' or 'old Māori taro'. The name and phrases were applied to what has been identified here as variant HR. *Taro potango* a name encountered only once in the field, was used by an elder Māori woman to name corms of variant RR harvested from a garden. These she also called 'real Māori taro'.

Taro hoia was the name most frequently encountered, and was raised in contrast to

taro cultivated in gardens. It is wild taro, or taro not eaten except for the leaves, and is green taro. Direct usage to describe plants in the field was unfortunately not met. Sometimes wild and cultivated taro were contrasted without the use of Māori names. Wild taro of the variant GP was referred to as not good for eating (though eaten by some), and as food for pigs (once also named *taro poaka*, in reference to pork). Variant GP, in addition, has predominantly green petioles so that the impression gained is that variant GP is in fact *taro hoia*.

However there is some confusion since wild taro of variant RR was once contrasted as a different type from cultivated plants of the same variant. It is possible that *taro hoia* could be thought of by some people as any apparently wild taro while others apply the name more closely to wild green taro, that is, variant GP (the variant which is predominantly wild in distribution — see Chapter Seven).

The above illustrates just some of the problems in establishing definitions for names. Other qualities were also used by people to distinguish types, notably colour and texture of the corm either before or after cooking. It was frequently unclear which state of cooking colour described, and sometimes even whether the colour mentioned described the leaf rather than the corm flesh.

The present equation of variant GP with *taro hoia*, though uncertain, corresponds with earlier records: Colenso (1880) writes of taro that ‘there are also more than twenty varieties or species, which, like the kumara, differed greatly in size, in quality, and in the colour of its flesh; besides one which is known to have been introduced since the time of Cook’s visit. This newer one is called *taro hoia*; it is a much larger root (tuber) and plant, and it is also coarser in its flesh, and is not so generally liked’.

Wilson (1894) states that ‘the great labour of growing *taro maori* caused it to be abandoned when the *taro Merekena* was introduced. The latter is hardy, prolific, runs wild in fact, and is easily cultivated, but it is very inferior in flavour and flouriness to *taro maori*’. Wilson’s description of *taro Merekena* matches in both growth habit and cultural status to present-day *taro hoia*, identified here as variant GP, and also matches Colenso’s (1880) description of *taro hoia* — including the claim for its recent introduction.

Another form of ‘*Merekena*’, namely ‘*merikana*’, is applied to a kumara variety supposed to have been brought on American whaling ships from the Pacific Islands (Best 1976). This raises the possibility that *taro Merekena* was not, in fact, recently introduced but for some reason received its name by transfer from the kumara variety. The reverse could, of course, be true or both taro and kumara varieties may have been introduced by American ships. A recently introduced variety from some other, perhaps unknown, source might also have been dubbed ‘American’ for want of any other name.

Further confusion is added by the possibility, indicated by J. Diamond (1982; pers. comm. 1984), that early descriptions of *taro Merekena* could refer to the aroid *Alocasia macrorrhizos*, which was apparently introduced last century as an ornamental, and is now commonly found as an ornamental or wild. The rampant growth habit of *Alocasia*, and its poor eating quality (A. Esler, DSIR, pers. comm. 1982), also fit the early descriptions of *taro Merekena*.

Cruise (1824), writing of his travels in 1820, states that ‘the taro plant, which has been imported from Otaheite, is cultivated by a few natives with much success’. This statement is ambiguous in that Cruise may be reporting Māori knowledge, or he may, like an earlier writer, be stating his own opinion of the origin (Tahiti). Nicholas (1817) states that ‘it does not appear to me that this plant is indigenous to New Zealand, but must, in my opinion, have been brought hither, either by Captain Cook or some other European navigator who has visited the country’. This example is given simply to illustrate an opinion; it is not being suggested that Nicholas influenced the statements of Cruise.

From the above, it is apparent that no definite conclusion can be drawn from written or oral history regarding the possible recent introduction of a named taro variety, early in the period of European occupation. The variety that may have been recently introduced may be variant GP. Of the three major variants, least information was obtained regarding Māori recognition of variant GR. When asked about a mixed patch of variant GR and RR one group seemed to not recognise the co-existence of two types (field notes, 3.2.83). Another informant knew that the non-cultivated clumps of variant GR in her garden were not ‘real Māori taro’, but could only speculate on its more distant origin (field notes, 8.2.83). A third informant whose plants came from a Māori cultivator some twenty years ago recollected that the ‘small green’ had been regarded then as sweeter and better than the red (variant RR), although not as big (field notes, 15.8.83). The scantiness of this information may simply reflect the rarity with which both variant GR and people were encountered at the same time during the field surveys. D. Yen (pers. comm. 1983) indicates that *makatiti* may be variant GR.

Conclusions

Written records of the Māori classification of taro are too incomplete to provide any clear suggestions regarding the number, and history, of botanically distinct variants existing in the recent or distant past. However, two easily debated suggestions can be made; firstly that the naming of variant RR as *taro maori* reflects a pre-European origin, and secondly that the naming of variant GP as *taro hoia* indicates that it was introduced by an American whaling ship early last century, from Tahiti.

A wide ranging and thorough etymological study of Māori plant classification would clarify the history of taro, but such an ideal cannot be reached. While ethnographic records are obviously inadequate, encounters during the recent fieldwork did give the impression that valuable knowledge does exist of old traditions associated with taro, mainly amongst the older Māori.

Appendix 10. Cytology

Ap. 10.1 Cytological methods

Preparation

(1) Use recently potted plants with actively growing roots. If plants are stripped of leaves and roots prior to potting, they will be found with suitable roots when the first new leaf is seen emerging. Root tips (1–2 cm) may be harvested at any time of day.

(2) Place tips in 0.2% colchicine (0.03 g per 15 ml distilled water) using sufficient volume to fully immerse the root tips. Leave at room temperature 2.5 to 4 h, aeration is not necessary. This is a very high concentration of colchicine and could perhaps be reduced to 0.02% without loss of effect. Generally, freshly made colchicine is used as it degrades with storage, allowing visible algal growth. The solution may be stored for short periods of some days at least, in a refrigerator, and may be re-used.

(3) Fix tips in 3:1 absolute ethanol/glacial acetic acid, at room temperature, for approximately 24 h. Theoretically, material can be left for longer (e.g., over a weekend) if put in a freezer, but in fact consistently good results were only obtained using freshly fixed tips.

(4) Soften the tips in 1M HCl at 60°C (waterbath) for 4 to 4.5 minutes. Thicker tips tend to need a little more time than thinner tips.

(5) Remove from acid and quickly place directly in small tube containing approximately 2ml (enough to fully immerse the tips) of Feulgen stain. Replace in dark for at least 10 mins or until the tip is stained bright purple.

(6) Remove the tip, cut off the end 1mm with root cap and meristem, and place it on a very clean slide.

(7) Place a very small drop of 45% acetic acid on the tip and with pointed needle begin maceration. Remove the tip epidermis. Place a drop of lacto-propionic orcein on the slide and continue maceration briefly. If the tip is too finely macerated, the time later required to search the slide fully under the microscope will be increased. If not macerated enough clumps of cells will prevent a good spread of chromosomes. The material should have approximately 0.5 mins in the stain before the next step, including the time for maceration.

(8) Put on coverslip and tap with a blunt needle to disperse clumps of cells and remove air bubbles. This is best done holding the cover slip down gently with fingers, with tissue paper between fingers and slide to mop up excess stain as it is squeezed out.

(9) Place slide between layers of blotting paper and squash coverslip onto the slide with very firm thumb pressure, shifting one thumb only while the other maintains the pressure. Any lateral movement of the coverslip will shear the cells into useless fragments.

(10) Label the slide, then inspect under the microscope. For counting, polarised light provides good contrast, but for photographs this contrast may result in difficulty in making prints in which the cell background isn't prominent. Also, better depth of field may be needed for a photograph if the spread isn't very flat — another reason to use bright field optics. The slide may be squashed again to improve the spread of

chromosomes.

(11) If the slide is well made, with no air gaps under the coverslip caused by dust, it may be left for a day or so without drying out. For permanent slides, the following procedure was used:

Hold the slide with tweezers and immerse it fully in liquid nitrogen, until the liquid nitrogen stops bubbling around the slide. Hold the slide in the air and breathe on the coverslip to warm it slightly, without fully melting the chromosome preparation. Place the slide firmly on bench and use a scapel blade to prise the coverslip off. Ideally it should snap off intact, so that time isn't spent removing fragments while the preparation melts. Place a drop of Euparal on the slide and put on a fresh coverslip. Place slide on a low-heat bar or leave at room temperature to dry.

Stain Recipes

Feulgen Stain:

- Leuco — basic fuchsin (modified formula after Darlington and La Cour, 1969).
- Dissolve 1g basic fuchsin by pouring it over 200ml of boiling distilled water.
- Shake well and cool to 50°C.
- Filter (Whatmans No. 1 paper) and add 30ml of HCl to the filtrate.
- Add 3g $K_2S_2O_5$ (or $Na_2S_2O_5$).
- Allow solution to bleach for 24h in a tight stoppered bottle, in the dark; add approximately 4g activated charcoal (for decolourising the solution) and filter (Whatmans No. 1 paper) the solution as fast as possible after addition of the carbon.
- Store in dark at $\pm 5^\circ C$. Ideally store in aliquots to reduce exposure to air, or in a concertined plastic bottle.

Lacto-Propionic Orcein:

- Mix: 5g synthetic orcein
50ml 45% propionic acid
50ml 45% lactic acid
- Boil in reflux condenser for 3 days, filter while warm and store in fridge (where precipitation will occur).
- Filter into small bottles after precipitation. Can be diluted with the 45% lactic and propionic mixture (see previous page).

Chemicals

acetic acid, analytical Reagent, BDH.

activated charcoal powder, Technical Grade, AJAX Chemicals, Sydney.

basic fuchsin, standard stain, product number 34032, BDH.

colchicine, product number 27805, BDH.

dichlorofluoromethane, 'arctic Air' Refrigerant 12, Hapi International Export, New Orleans, LA 70119.

ethanol, Analytical Reagent, BDH.

lactic acid (source not known).

synthetic orcein (source not known).

propionic acid (source not known).

sodium metabisulphite, UNILAB laboratory reagent, AJAX Chemicals, Sydney.

Ap. 10.2 Cytological observations of New Zealand taro (five variants from 17 localities)

Dyer (1979) states that surveys of root tip cells indicate that mutant karyotypes produced by mitotic errors rarely occur with a frequency greater than 0.05%. It appears generally accepted (D. Goates, Research School of Biological Sciences, A.N.U., pers. comm. 1983) that very few observations of root tip cells are required for accurate counts. The counts presented below are for cells observed with the maximum number of chromosomes for each plant accession. Many ruptured cells were observed with less than the maximum number of chromosomes, due to excessive spreading, and are not recorded here (although some were photographed).

Variant	Plant accession number	Botany department site number	Site type	Locality	Region	Root tip	Cell number	2n chromosome number	
RR	AKL 27	N15/8	Wild	Okokako Road	Central Bay of Islands	1	1	42	
						2	1	42	
							2	42	
	AKL 48	N8/10	Wild	Waiti Bay	Cavalli Islands	1	1	42	
							2	42	
							3	42	
							4	42	
	AKL 55	N259/6	Wild	Whangapoua Beach	Great Barrier Island	1	1	42	
							2	42	
							3	42	
	AKL 62	N63/3	Garden, non-cultivated, non-derelict	Te Hekawa	East Cape	1	1	42	
							2	42	
						2	1	42	
	AKL 65	N61&60/2	Wild	Hamana Stream	East Cape	1	1	42	
							2	1	42
							3	1	42
	AKL 70	N18&22/2	Garden, non-cultivated, non-derelict	Waimamaku	South Hokianga	1	1	42	
							2	42	
						2	1	42	
RR	AKL 84	N35/1	Garden, non-cultivated, non-derelict	Port Charles	Coromandel	1	1	42	
							2	42	
							3	42	
						2	1	42	
						2	42		
GR	AKL 61	N63/4	Garden, non-cultivated, non-derelict	Te Hekawa	East Cape	1	1	42	
							2	42	
						2	1	42	
							2	42	

	AKL 69	N18&22/2	Garden, non-cultivated, non-derelict	Waimamaku	South Hokianga	1	1	42
						2	1	42
							2	42
							3	42
						3	1	42
						4	1	42
	AKL 83	N3&4/1	Garden	Waihope Lake	Aupouri Peninsula	1	1	42
							2	42
							3	42
GR	AKL 85	N39/4	Garden, non-cultivated, non-derelict	Colville	Coromandel	1	1	42
							2	42
GP	AKL 17	N1&2/2	Wild	Kapowairua (Spirits Bay)	North Cape	1	1	42
						2	1	42
							2	42
						3	1	42
							2	42
	AKL 23	N15/4	Wild	Ngawha	Central Bay of Islands	1	1	42
							2	42
							3	42
							4	42
	AKL 63	N70/4	Wild	Rerepa Stream	East Cape	1	1	42
							2	42
	AKL 30	N11/2	Wild	Te Arakanihi	Coastal Bay of Islands	1	1	42
							2	42
							3	42
						2	1	42
AKL 34	AKL 34	N24/2	Garden	Manganese Point		1	1	28
							2	28
AKL 79	AKL 79	NIO9/1	Garden	New Plymouth	Taranaki	1	1	28
							2	28
							3	28
							4	28
						2	1	28
						3	1	28

Appendix 11. Ribulose-1,5-bisphosphate carboxylase

Ribulose-1,5-bisphosphate carboxylase-oxygenase (E.C.4.1.1.39) is the major soluble leaf protein in plants, and catalyses the initial step in Calvin's reductive pentose phosphate cycle. The genetics and physiology of the enzyme have been reviewed by Mizioroko and Lorimer (1983).

RuBP carboxylase has been purified to homogeneity from a variety of plant, algal, and bacterial sources. All of the plant and algal enzymes studied to date are of similar molecular weight (560×10^3 daltons) and contain eight large (56×10^3 daltons) and eight small (14×10^3 daltons) subunits (Mizioroko and Lorimer 1983). The large subunit is encoded by chloroplast genomes and the small subunit by the nuclear genome (Kung 1976). The reported heterogeneity (multiple bands of dissociated subunits on isoelectric focusing gels) in both large and small subunits has been the basis for use of the enzymes in numerous studies of phylogeny (for example, Kung 1976; Uchimiya et al. 1977; Gatenby and Cocking 1978) and of cytoplasmic inheritance after *in vitro* protoplast fusion (for example, Melchers et al. 1978; Shepard et al. 1983).

The published methods for the extraction, purification and characterisation of RuBP carboxylase vary widely and no one method appears applicable to all species. Chen et al. (1976), for example, obtain and purify the protein by 1) crystallisation in clarified leaf sap (*Nicotiana*, *Solanum*, and *Petunia*); 2) salt fractionisation and column chromatography (a wide range of genera including *Chlamydomonas*, *Selaginella*, and *Spinacia*) and 3) by specific absorption to a column of immobilised antibodies that had been raised against RuBP carboxylase from *N. tabacum* (*Ginkgo*, *Beta*, and *Triticum*).

Oxidation and reactions of proteins with polyphenols are problematic during extraction and the following procedures. The combinations and amounts of protective reagents (sodium metabisulphite, mercaptoethanol, polyvinylpyrrolidone-40, and NaCl to name a few) used during extraction, purification and characterisation vary widely and generally without explanation. O'Connell and Brady (1981) have demonstrated that the widely reported heterogeneity (charge diversity) of three large subunit polypeptides is an artefact of carbamidomethylation of the enzyme before isoelectric focusing, a reaction routinely performed in previous studies of RuBP carboxylase. They report that the simplest isoelectric focusing patterns were observed when the enzyme was isolated rapidly and gently by immunoprecipitation or preparative PAGE.

No published method for the extraction and purification of RuBP carboxylase from *Colocasia* exists. During the present study of *Colocasia esculenta* in New Zealand an unsuccessful effort was made to develop a rationalised procedure for extraction, purification and characterisation of the leaf protein. Extraction and purification procedures tried included:

- (1) crystallisation in clarified leaf sap;
- (2) extraction with a range of NaCl concentrations in the extraction buffers;
- (3) differential precipitation by heat treatment;
- (4) immunoprecipitation with antibodies raised against commercially purified RuBP carboxylase from *Spinacia* (spinach);

- (5) purification on a G-200 Sephadex column;
- (6) preparative PAGE.

The outcome of these trials were:

- (1) No crystallisation was observed;
- (2) Low concentrations of NaCl (0.1 to 0.4M) had no noticeable effect on yield as determined by SDS-PAGE of SDS-dissociated extracts. With 4M NaCl, yield was no better or less than with extraction in 0M NaCl, although other effects of unknown basis were observed in the comparisons with SDS-PAGE.
- (3) Heat treatments of clarified sap extracts precipitated RuBP carboxylase along with other proteins, as shown by SDS-PAGE of treated and untreated extracts.
- (4) The antibodies raised precipitated saline (0.14 M NaCl) solutions of the original antigen, and showed high titre, but did not precipitate protein from *Colocasia* leaf sap diluted with saline solution.
- (5) Only poor separation of RuBP carboxylase was achieved, indicated by a skewed λ^{280} Peak (for eluate passed through a continuous-flow spectrophotometer), and shown by SDS-PAGE of the contents of eluate fractions.
- (6) Good purification was achieved with non-dissociating PAGE in gels of large pore size, but a satisfactory procedure for excising or eluting the purified protein from the gels and transferring it to an isoelectric focusing gel was not established. Purity was shown by direct staining of non-dissociating gels or by applying these as samples for SDS-PAGE with slab gels and then staining.

Isoelectric focusing was achieved with RuBP carboxylase purified from *C. esculenta* using preparative gel electrophoresis. However, the procedure was poor and likely to have caused artefacts, and was not repeated.

Comparative SDS-PAGE of clarified and sap extracts of *C. esculenta* variants RR, GR, and GP, and *Brassica oleraceae* var. *capitata*, alongside molecular weight standards, showed the RuBP carboxylase subunits to have uniform molecular weights, i.e., large subunits: approximately 50×10^3 daltons; small subunits: approximately 12.4×10^3 daltons.

Appendix 12. Earliest European description of taro in Queensland, Australia

The following description was transcribed by the present author from a 1980 facsimile of the daily journal of Joseph Banks (Banks 1770, *The Journal of Joseph Banks in the Endeavour, Volume Two*, with a commentary by A.M. Lysaght; Surrey, England, Genesis Publications and Rigby Ltd; pp. 203–4).

Endeavour River, 27th June, 1770. Some of the gentlemen who had been out in the woods yesterday brought home the leaves of a plant which I took to be Arum esculentum the same I believe as is called Cocos in the West Indies in consequence of this I went to the place & found plenty on tryal however the roots were found to be too acrid to be eat the

leaves however when boiled were little inferior to spinage in the same place grew plenty of Cabbage trees & a kind of Wild Plantain whose fruit was so full of stones that it was scarce eatable another fruit about as large as a small golden pippin but flattened of a deep purple colour there when gathered off from the tree were very hard & disagreeable but after being left a few days became soft & tasted much like indifferent damsons.

28th June. Tupia by roasting this Cocos very much in his oven made them lose intirely their acridity the Roots were so small that we did not think them at all an object for the ship So resolvd to content ourselves with the greens which are called in the West Indies Indian kale. I went with the seamen to show them the Place & Gathered a large quantity. saw one tree and only one notched in the same manner as those at Botany bay....

Note: Banks makes no reference on the 26th of June to the excursion mentioned at the start of his entry for the 27th of June. The purple fruit mentioned here is later identified in his general account of New Holland (Australia) as *Ficus caudiciflora*. Also in this general account he describes Indian kale (*Arum esculentum*) [syn. *C. esculenta*] as occurring in 'tolerable plenty', without reference to specific location. This suggests that he saw it at more than one site. Taro was recorded again in the Endeavour River area during the nineteenth century, the early twentieth century, and in 1987 (Appendix 16).

Appendix 13. Specimens of *Colocasia* spp. seen in European Herbaria

Collection records for three species of *Colocasia*, found at European herbaria in 1984/85: location, date in brackets, collector's name in italics, field number (or herbarium number), and herbarium locations in brackets. Abbreviations for herbaria: B = Berlin (Dahlem), BM = British Museum, E = Edinburgh, K = Kew, L = Leiden, LG = Leningrad, P = Paris. Authorities for determinations are given where possible. All specimens were seen by P. Matthews. Additional records, not from herbaria, are noted for *C. gigantea*. See Appendix 16 for full list of herbaria searched.

C. fallax Schott (Engler and Krause 1920)

Pir Pauce, Khasia Hills, India (1850), *Hooker and Thompson* (K, type), det. Schott; Darjeeling, India (1875), Clarke 29237 (K), det. anon; Himalayas, India (pre-1893), ex hortus Herrenhausen, Engler 240 (K, B, LG), det. Engler; Dehra Dun, N.W.P., India (1898), Gamble 26994 (K), det. anon; Dehra Dun (1898), Gamble 27041 (K), det. anon; Singbhum, India (1900), Haines 318 (K), det. Haines; Garhwal Dun, W. Himalaya, India (1902), Jacquiel 27017 (K), det. anon; Ranchi/Palaman, India (1918), Haines 4440 (K), det. Haines; Lidi Khola, Nepal (1954) *Stainton, Sykes & Williams* 6801 (BM), det. Nicolson; Shidam Khola, Walna, Nepal (1954), *Stainton, Sykes & Williams* 5165 (BM), det. Nicolson.

C. affinis Schott (Engler and Krause 1920)

Khasia Hills, India (1850), *Hooker* 470 (K, type), det. Schott; Sikkim, India (1850?),

Hooker (K), det. anon; Sikkim, India (1857), *Hanson* 755 (LG), det. anon; Kenseng (?), India (1876), *Gamble* 854A (K), det. anon; Pankabari, Sikkim, India (1879), *Gamble* 7018 (K), det. anon; Sikkim, India (1881), *King* (K), det. *King*; Manila, Philippines, recorded as exotic (1892), *Loher* 2435 (K), var. *jenningsii* Veitch, det. Brown; Prome Road, Rangoon (1932), *Parkinson* 1478 (K), det. Parkinson; Doi Chiengdao, SW of Ban Tam, Thailand (1935), *Garrett* 977 (K), det. Garrett; Prome Hills on the Irrawaddy, Burma (1936), label B attached to *Wallich* 8952A (LG), Silhet, India, *Wallich* 8952A (LG), det. Engler and Krause (1920); Manipur, India (1945/46), *Bullock* (K), c.f. *affinis* det. Sivadasan (P. Matthews: this is almost certainly *C. affinis* var. *jenningsii*); Pasay City, Philippines, recorded as an ornamental (1955), *Steiner* 683A (L), *C. esculentum* det. anon (P. Matthews: the leaf colour pattern indicates *C. affinis* var. *Jenningsii*); Doi Suthep, Chiangmai, Thailand (1968), *Larsen, Santisuk & Warncke* 2588 (L), det. Sivadasan; Dharan, Nepal (1972), *Dobremez* 1435 (BM), var. *jenningsii*, det. Nicolson.

***C. gigantea* Hook f. (Hotta 1970)** — including specimens identified as *C. indica* (Lour.) Hassk., a synonym used by Engler and Krause (1920)

Java (pre 1844), *collector illegible* L 898.88 381 (L), det. Bakhuizen v.d. Brink; Java (1857), *Zollinger* (B, K, BM), det. Engler & Krause (1920); Java (19th century), *Zollinger* 472 (LG, P), *C. indica* Kunth det. anon (P. Matthews: fruiting heads and blade look like *C. gigantea*); Dong-Tom, ?Vietnam (1889), *collector?* 2035 (P), det. anon; Hanoi, Vietnam (1890), *collector?* 4525 (P), det. Engler; Balu Caves, Selangor, Malay Peninsula (1896), *Ridley* 8156 (K), det. Ridley?; Rambang, Java (1896); Hong Kong (1905), *Cavalerie* 2506 (E), det. Nicolson; Biutenzorg, Java (1912), *Koorders* 40420B (L), det. Backer; Bienhoa, Chua Chong, Cochinchina (Vietnam) (1914), *Chevalier* 29866 (P), det. Chevalier; Besoeki vic. Kalibendo, Java (1916), *Koorders* 43956B (L), det. Koorders; Qua Nenck, Kelantan, Malay Peninsula (1924), *Nur & Foxworthy* 11910 (K), det. Henderson; Sisawat, Kanburi, Thailand (1926), *Kerr* 10165 (E, K, P), det. Nicolson; vie. Chumphon/Chumpawn, Thailand (1927), *Kerr* 11576 (K, P), det. Nicolson; Thailand (1929), *collector?* 202 (P), det. anon; Hainan, China (1932), *Lau* 490 (K), det. Nicolson; Annam-Cua-Tung, Indochina (1935), *Cadiere* (P), det. anon; Ch'uan District, Northern Kwangsi, very rare (1937), *McClure* 20567 (K), det. Nicolson; ?Annam or Dong Tam, ?Indochina (1939), *Poilane* 30165 (P), det. Nicolson; Bank Khen, central Thailand (1960s?), *Buneiuai & Nimanong* 38126 (L), det. illegible; Khao Chong Forestry Station, Trang Prov., S.W. Thailand (1962), *Nicolson* 1721 (B, E, K, P), det. Nicolson; Ma On Shan, Hong Kong (1969), *Shiu Ying Hu* 6490 (K), det. Shiu Ying Hu; 40 km south of Chumphon, Thailand (1971), *Bogner* 427 (K), det. *Bogner*; Szemao, China (date?), *Henry* 12379 (K), det. anon (P. Matthews: inflorescence immature, blade typical for the species); Sumatra (date?), *Jacquinot* 472 (P), det. Nicolson.

Note: Hotta (1970, 1983) reports that *C. indica* (syn. *C. gigantea*) is widely distributed from Malaysia to Borneo and Java, and that it is cultivated in Japan. During the present study, live collections of *C. gigantea* were obtained from Colombo in Sri Lanka (1986) *Amarasinghe*, ANU T321; Rayong, Chantaburi, Chonburi, Thailand (1986), *Yen* 6, ANU T357; and Hoshidate, Iriomote Is., Okinawa Islands, Japan (1982),

Kobayashi & Sakamoto 82.1.18.1.1, ANU T311.

Appendix 14. Poorly defined and poorly known species of *Colocasia*

Records from a survey of European herbaria, 1984/85. The collector surname is in italics, and is followed the collector's field number if available. Abbreviations for herbaria, given in brackets, are: BM = British Museum, B = Berlin (Dahlem), E = Edinburgh, G = Geneva, K = Kew, L = Leiden, LG = Leningrad, P = Paris. Authorities for determinations (det.) are given where possible.

Species and or genus not determined with certainty by original collector, later taxonomists, or by P. Matthews

Taiwan, vie. Taihoku, *Tanaka* 5336 (L), *Colocasia gigantea?* (Bl.) Hk.f., det. Nicolson; Himalaya, Sikkim, *Treutler* (LG), *Colocasia* sp, det. *Treutler* (blade with shallow sinus and front lobe v. long); Thailand, Chiang Mai Province, *Nicolson* 1650 (P, B), *Colocasia* sp, det. Nicolson; Burma, Upper Chindwin, *Lace* 4197 (E), *Colocasia* sp, det. Nicolson; India, Bengal, *Sinclair* 4274 (E), *Colocasia* sp, det. Nicolson; India, East Bengal, *Griffith* (East India Company) 6007 (K), *Arum nymphaeifolium?* (syn. *C. esculenta* var *nymphaeifolia?* (Vent.) Engl. in Engler & Krause 1920), det. Griffith?; Nepal, Churia Hills, *Williams & Stainton* 8231 (BM), *Colocasia?* new species?, det. Nicolson; China, Yunnan *Houa-Kiang* 7505 (E), *Colocasia?*, det. Nicolson; Thailand, Knwae Noi River Basin, *Kostermans* 1394 (L), *Colocasia esculenta?* (L.) Schott, det. Nicolson; Thailand, Mae Rim, *Larsen, Santisuk & Warncke* 2475 (E), *Colocasia* sp, det. Bogner; Thailand, Dai Chiengdao, *Garrett* 1229 (K), *Colocasia* sp, det. Garrett; Thailand, Doi Soo-tep, *Nicolson* 1650 (K, P), *Colocasia* sp, det. Nicolson; Thailand, Chiengmai, *Larsen, Santisuk, Waracke* 2588 (E), *Colocasia* sp, det. Bogner. India, Darjeeling, *Clarke* 26956 (K), c.f. *C. fallax*, det. Clarke; India M (meridional = southern), *Wallich* 8948B (LG), *C. indica*, det. anon (P. Matthews: could be *C. gigantea*, specimen an inflorescence only); Southern Burma, Tavoy District, vie. Paungdau, *Keenan, Tun Aung, & Rule* 1664 (E), *Colocasia* c.f. *affinis*, det. Bogner; Hong Kong, *Cavalerie* 2136 (E), *C. gigantea?* (Bl.) Hk. f., det. Nicolson; Nepal, vie. Muna, *Stainton, Sykes, & Williams* 4067 (BM), *C. affinis* Schott?, det. Nicolson; Vietnam, Hanoi Botanical Gardens, *Zonkin* (L), ?*Colocasia gigantea*, det. Nicolson.

Previous identification questioned by P. Matthews, with possible alternative identifications suggested in brackets

Java, *Lauterbach* 6060 (G), *Alocasia indica* Schott?, det. Lauterbach (*Colocasia* sp, peltate blade); Himalaya, Silhet, *Wallich* 8944 (LG), *Colocasia fallax* Schott, det. Engler & Krause (1920), (*Colocasia?* blade with v. shallow sinus and front lobe v. long); Bangladesh, Kushtia district, *Khan & Hug* 3935 (E), *Colocasia esculenta* (L.) Schott, det. anon (*C. gigantea?*, spathes white); India, Middle Andamans, *Bhargava* 2822 (L), *Colocasia esculenta* (L.) Schott, det. Sivadasan (*Alocasia?*, blade narrow with deep sinus); India, *Buchanan-Hamilton* 63 (BM), *Arum rupestre*, det. Buchanan-Hamilton

(*Colocasia?*, not *C. esculenta*, peltate blade with v. shallow sinus); India, Calcutta, *Clarke* 33593 (G), *Colocasia antiquorum* Schott, det. Clarke (*Colocasia?*, blade narrow elongate with deep sinus); Thailand, Phu Luang, *Phusomsaeng & Bunchuai* 27 (L), *Alocasia* sp, det. anon (*Colocasia* sp, small peltate leaf with shallow sinus).

Poorly known species

Sumatra, Padang Province, *Becarri* (B), *Colocasia gracilis* Engl., det. Krause (type for Engler & Krause 1920); India, upper Assam at Makum, *Mann* (K), *Colocasia Mannii* Hook. f. (type for Engler & Krause 1920); India, Bengal, *Roxburgh*, illustration for *Roxburghiana*, Aroideae (K), *Colocasia virosa* Kunth, det. Engler & Krause (1920).

Appendix 15. Canberra Taro Collection

Source collections and collectors for the Canberra Taro Collection, 1981–88 (also known as the ANU Taro Collection).

Institutional sources

- (1) Department of Prehistory, Research School of Pacific Studies, Australian National University, Canberra: D. E. Yen, P. J. Matthews.
- (2) Australian National Botanic Gardens, Canberra: I. Telford.
- (3) Melbourne Botanic Gardens, Melbourne: S. Forbes.
- (4) La Trobe University, Melbourne: Y. Fripp.
- (5) Royal Botanic Gardens, Sydney: J. Forlonge.
- (6) Western Australian Herbarium, Perth: K. Kineally.
- (7) Arid Zone Research Institute, Northern Territory Conservation Commission, Alice Springs: P. Latz.
- (8) Brisbane Botanic Gardens, Brisbane: D. Shaw.
- (9) Department of Agriculture, Lae Technical University, Papua New Guinea: A. Gurnah.
- (10) Dodo Creek Research Station, Honiara, Solomon Islands: R. Liloqula.
- (11) Kyoto Plant Germplasm Institute, Faculty of Agriculture, Kyoto University: T. Kawahara.

Collectors, by country or area

- (1) Australia: D. Yen, R. Jones, P. Latz, D. Rentz, R. Hinxman, R. Collins, P. Randal, N. White, N. Scarlett, S. Forbes, K. Kineally, A. Marchant, D. Rowell, K. Thiele, P. Matthews.
- (2) Papua New Guinea: A. Gurnah, P. Lea, M. Quinn, D. Yen, J. Golson, P. Matthews.
- (3) Solomon Islands: D. Yen, M. Patel.
- (4) Vanuatu: P. Ottino.
- (5) Polynesia, including New Zealand: D. Yen, P. Matthews, D. Spennemann.
- (6) Timor: D. Yen.

- (7) Sri Lanka: V. Amarasinghe.
- (8) Nepal: H. Yoshino, S. Sakamoto.
- (9) Madagascar: H. Wright.
- (10) Thailand: D. Yen.
- (11) Philippines: D. Yen, H. Conklin.
- (12) Japan: K. Fukui, H. Kobayashi, T. Kawahara, R. Terauchi, P. Matthews.

Appendix 16. Records of wild taro in Papua New Guinea, 1936 to 1985

Herbarium records of wild taro in New Guinea, and 1985 field survey records from Morobe Province, Papua New Guinea. Inspection dates and abbreviations for herbarium names are given in Appendix 17.

1936, June Fly River Expedition of the American Museum of Natural History; Palmer River, an upper tributary of the Fly River, Papua New Guinea; BRI 380777, with inflorescences; gregarious in patches on muddy riverbanks.

1961, 14 October D. Nicolson; Sogeri Rubber Estates, approximately 30 miles east of Port Moresby, Papua New Guinea; B, D.N. field number 1439, with fruit and seed; locally abundant in wet areas, stolons over 1 m long.

1961, 18 November D. Nicolson; Nanokwari, road to Tafelberge, west New Guinea (Irian Jaya), at 30 m altitude; P 23366, with fruit, B field number 1569 with inflorescence; occasional stoloniferous herb in secondary regrowth on limestone.

1964/5 A. Jermy; Buimo Creek northeast of Lae, Morobe Province, Papua New Guinea; BM, A.J. field collection number 4460, with inflorescences; along riverbank in marshy situations, in fairly well worked alluvial soil with much humus. Root-stock short, thick, with stolons.

1971, 24 July H. Dosedla; Mount Hagen, also Mount Kuta to 2100 and 2300 m, Western Highlands, Papua New Guinea; P 16679, inflorescence; in rain forest understory, preferring light places; vernacular names '*kumgmb*' (Hagen language) and '*talagh*' (Enga language); plants not used by people.

1985, 29 June P. Matthews; Wau road between Lae and Wampit, foot track to Geb stream; field site 29/6/1; stoloniferous, scattered alongside track to gardens and cocoa plantation belonging to Gabensis Village, in forest with trees to 10 m, but cleared along track.

1985, 29 June P. Matthews; Wau road between Lae and Wampit, above the southeastern extension of swamp at the head of Garagos River; scattered plants interconnected by stolons to greater than one metre length, in shallow flowing creek in

gully with remnant forest, on south side of the road, below steep kunai grassland; Canberra live collection T227.

1985, 29 June P. Matthews; Wau road between Lae and Wampit, at edge of alluvial flats of the Markham River; field site 29/6/4; stoloniferous, in slashed clearing alongside road, at edge of forest, absent from the immediately adjacent forest. *Alocasia macrorrhizos* (? *flabellifera* A. Hay) was scattered alongside the road and within the forest, and *Xanthosoma sagittifolium* (definitely feral, exotic introduction) was also scattered alongside the road.

1985, 29 June P. Matthews; Rumu River, approximately 2 km north of Markham Highway; field site 29/6/5 (see Figure 10.10); stoloniferous, flowering plants in muddy bank of stream at edge of the main river, and at fringe of remnant forest with swidden gardens, with no gardens immediately adjacent to the wild taro; leaves edible, corm not ('i nogut kaikai', middle-aged male informant); Canberra live collection T229.

1985, 4 July P. Matthews; Markham Highway junction with road to Ngasawampum Village; field site 4/7/1; stoloniferous, some with fruit and seed, in forest garden regrowth immediately adjacent to highway, the same variety also in ditches alongside the Markham Highway east of the junction, and in forest on east side of road to the village; according to local informant, an elderly man, the leaves are edible (cook, discard water, cook again), and the plants spontaneous ('wail taro, i kamap nating'). Canberra live collection T226.

1985, 5 July P. Matthews; Leron River valley, road to Sirasira, foot track from Nariyawan village to gardens; field site number 5/7/1 (see Figure 10.9); stoloniferous, in wet forested gully below swidden gardens on steep hill slope, between crossing of stream by the foot track and a bamboo water fountain at the head of the gully. Stoloniferous cultivars were noted in the gardens nearby; vernacular name for wild taro 'umanmumin'; Canberra live collection T225.

1985, 5 July P. Matthews; Leron River valley, road to Sirasira village; field site 5/7/4; stoloniferous, some with fruit and seed, at intersection of stream and road, below a permanent spring in forest remnant, in area of grassland. Taro with pink basal ring, and associated with feral *Xanthosoma sagittifolium*. The taro was spontaneous and inedible, according to local male informants. The spring is used by villagers as domestic water source, and cultivated taro could have been peeled at this site for cooking, giving rise to a feral colony.

1985, 16 July P. Matthews; Labutali, c. 14 km southwest of Lae, Pipi stream below Disina mountain; field site 16/7/1 (see Figure 10.9); stoloniferous, flowering plants along both sides of stream in forest, stolons to more than one metre length, this wild variety known locally as 'kiniku', and is phenotypically distinct from the differently named

varieties inspected at gardens upstream, at Puwamu. *Kiniku* was said to catch on trees and grow on banks in streams further inland, Naligi and Powatu, upstream from Puwamu, as well as being washed down to the beach (elderly male informants). The leaves and corms of *kiniku* are not eaten.

1985, 18 July P. Matthews; tributary on north side of Bwusi River, c. 25 km south of Lae and c. 2 to 3 km inland from beach, a short distance upstream from Bwusi village; field site 18/7/1; occasional clumps of stoloniferous taro on banks, some flowering, stream narrow and subject to flooding, with frequent log jams. 'Ngasange' was a name given for wild taro, in reference to plants collected by informants from an unseen site near Bwusi village.

1985, 20 July P. Matthews; base of Salamaua Peninsula, on south side between sago swamp and track to Salamaua village; field site 20/7/1; two varieties at edge of swamp, both stoloniferous and flowering, both unvariegated, one with white basal ring and green petiole (similar to the common wild phenotype elsewhere in the vicinity of Lae), the other with pink basal ring and green to purple petiole.

1985, 20 July P. Matthews; Francisco River, south of Salamaua, c. 1 km from river mouth; field site 20/7/3; stoloniferous, some with fruit and seed, scattered in kunai grass at boggy edge of river, below path to gardens along south side of the river from Logui village. Two old men from this village described the wild taro location on the Francisco River ('bikpela wara') and reported further sites on tributaries ('liklik wara').

1985, 22 July D. Yen; Wau road, c. 40 km from Lae, near Mumeng; stoloniferous, flowering plants on stream bank in forest clearing.

Appendix 17. Records of wild taro in Australia, 1770 to 1989

The following records come from herbarium collections, published and unpublished reports, and the present author's fieldwork and correspondence. Searches were made for specimens in the following European herbaria, in 1984 and 1985: Berlin, Dahlem (B), British Museum (BM), Edinburgh, Geneva, Kew (KEW), Leiden (L), Leningrad, Paris (P), Vienna, Warsaw. Searches for herbarium specimens in Australia and Papua New Guinea were made in the years 1985 to 1988: Atherton, Queensland (QRS); Brisbane (BRI); Australian National Gardens, Canberra (CBG); CSIRO, Canberra (CANB); Darwin (DNA); Lae, Papua New Guinea; Melbourne (MEL); Perth (WA); Sydney (NSW). Collection details are noted in the following order: date, collectors, location, herbarium or field number and a descriptive note (if stolons or inflorescences are present); and collectors' field notes.

Synonyms for *Colocasia esculenta* (L.) Schott are noted if not associated with a herbarium specimen sighted by the present author. All the identifications of the species are by either P. Matthews, after direct sighting of living or herbarium specimens, or by

reliable authors and correspondents. Identifications of the Jiyer phenotype (Figure 10.1) were all based on living plants seen by P. Matthews. The listing excludes a small number of records of plants that were definitely not wild, and/or were definitely not of the Jiyer phenotype. Most of these records were for urban or house-garden situations, or for unprovenanced plants located in botanical gardens.

Two letters received in 1987 from Robert Tucker (first with the Department of Parks and Recreation, Council of the City of Townsville, Queensland, and then Project Co-ordinator for the Townsville Palmetum) are presented in their entirety after the list of site records. These letters contain ethnographic information which should only be cited after consultation with R. Tucker. The first letter (1st June) convinced the present author of the necessity to survey wild taro in Queensland. The second letter was received in response to a report to R. Tucker on that fieldwork.

1770 Banks and Solander; New Holland: P 33, with inflorescence, MEL 1560158, with inflorescences. Banks (1770:203–04) describes the discovery and trial as a food of *Arum esculentum* (= *C. esculenta*) near the Endeavour River (Queensland), 27–28 June 1770.

1800–10 G. Caley sn; location not given; BM 191/?

1802 Brown (1830; 1960 fascimile) records *Calladium* acre (= *C. esculenta*) from tropical Australia (coast of Queensland and the Northern Territory, westward to Arnhem Land). Brown describes floral characters in some detail. Brown's east coast collection sites (W. Stearn, introduction to the 1960 fascimile), seem unlikely locations for taro, and the observation was probably made at the northern end of Cape York, or in the Gulf of Carpentaria.

1844–45 Leichardt (1847) records *Caladium* (= *C. esculenta*, or *Alocasia*) in his diary for May 11th (dry season), in creeks full of water and associated with rich grass, *Pittosporum* scrub, native mulberry, fig tree, several vines, *Polypodium*, and *Osmunda*. The area of this observation was many kilometres inland, west of Rockingham Bay, Queensland.

1858–66 A. Thozet; Cooktown or vicinity, Queensland; MEL 1560160 with inflorescence (material grown by Thozet after being received from another person).

1860–71 Dallachy; Rockingham Bay, Queensland; MEL 1560162, MEL 1560163 with inflorescence, KEW no number (date 1871?).

1863 or soon after. A. Dietrich; Port Denison (Bowen), Queensland; MEL 1560164.

Pre-1866 Fitzalan; Mount Elliot (probably near Townsville) Queensland; collection cited as *C. antiquorum* (taro) by Mueller (1865–66).

1877 Fitzalan; Port Denison (Bowen), Queensland; MEL 1560161.

1882 Persietz; Endeavour River, Queensland; MEL 1560159 with inflorescence.

1873 G.E. Darymple, reports large areas of 'Tara grubbed up by blacks' on the Johnstone River, northeast Queensland (Darymple 1874:615; not seen, citation pers. com. N. Horsfall). 'Tara' is a synonym for *C. esculenta*, and was often used by Europeans in the nineteenth century.

1883 Holtze; Port Darwin, Northern Territory; two sheets, MEL 1560165 with

inflorescence and MEL 1560166 with inflorescence (field number 188).

1891–93 G. Podenzana; Queensland; BM 191/70.

1889 F.M. Bailey (1889) reports in an unpublished manuscript that *C. antiquorum* (*C. esculenta*) grows wild by Harvey's Creek and by the Mulgrave River, Bellenden-Ker, Queensland.

1901 Roth (1901) reports that the corm of *C. antiquorum* (*C. esculenta*) is eaten by Aborigines at Cooktown, Cape Bedford, and in the hinterland and coast of Princess Charlotte Bay (all Cape York, Queensland). Bailey (1902) cites Roth for a record of taro from the Middle Morehead River (hinterland of Princess Charlotte Bay).

1907 N. Holtze; photograph of wild taro on stream bank, vicinity of Port Darwin. See plate titled 'Duck pool in the jungle' (Searcy 1907:98). Behind a large patch of taro, a tall stand of *Pandanus* is visible.

1918 G.J. White; Malanda, Cook District, Atherton Tableland, Queensland; BRI 011517.

1921, 31 August C.A. Gardner; near Mount Learning, King Edward River, Kimberley, Western Australia; WA, field number 1552; Gardney (1923) records that *C. antiquorum* (*C. esculenta*) forms dense colonies in humid valleys, in swampy black soil near Mount Learning, by the lower part of King Edward River. Gardner (ibid) notes that flowers were not seen, and that this was the first record of taro for Western Australia.

1936, 25 October H. Flecker; Freshwater River (near Cairns, Queensland); QR 042744 with inflorescence.

1966, 27 March B. Hyland; Cannabullen Falls, North Kennedy, Queensland; BRI 141536; KEW, two sheets, field number 03793. Upper tributary of Tully River, 17°41'S 145°32'E

1968, 11 April R.W.; Holme's Jungle, Darwin, Northern Territory; DNA 16611 with stolon; growing in water or mud, silty substrate, creek bank, and swamp.

1969 February D. Wheelwright; 12°25'S 130°50'E, Holme's Jungle, Darwin, Northern Territory; DNA, field number D2880, with inflorescence; in rainforest.

1972 I. Crawford; Mitchell Plateau, west of Kalumburu, Kimberley, Western Australia; WA, field number 41/72.

1972, 3 June J. Wrigley and I. Telford; 16°58'S 145°32'E, 13 km from Mareeba towards Kuranda, Cook District (Atherton Tablelands), Queensland; CBG 047693; on creek bank in open forest. Canberra live collection T32.

1972, 11 June J. Wrigley and I. Telford; 16°15'S 145°18'E, Stewart Creek (tributary of the Daintree River), near Mossman, Cook District, Queensland; CBG 043048; in mud beside creek, fringe of rainforest. Canberra live collection T33.

1973, June I. Crawford; Kalumburu (vicinity of a mission station), Western Australia; two sheets, WA field number 108.

1974, October D.R. Harris (1975, 1977:433); Lockhart, Cape York, Queensland; wild, regarded locally as native to the area, corm eaten.

1975, 12 April C. Dunlop; 12°24'S 130°59'E, Holme's Jungle, Darwin, Northern Territory, DNA 10728 with inflorescence; L 467759 with inflorescence; in black clay with fresh running water, margin of jungle and coastal plains, rhizomatous, the stems

above and below ground.

1975, 20 August A.S. George; approximately 15°02'S 126°40'E, Colocasia Creek, Worriga Gorge, Drysdale River National Park, Kimberley, Western Australia; WA field number 14083; rhizomatous herb, in black loam in and beside creek, in low woodland; photographs show cycads adjacent; patch relatively small, consisting of several dozen plants, well established in permanent seepage in a shady area below a cliff, at the upper end of the gorge (pers. coma. 1987).

1980 R. Jones; Mitchell Range, Northern Territory, CBG 8104695; Canberra live collection T30, external characters fit Jiyer phenotype.

1980 R. Jones; 80 km east of Maningrida, Arnhem Land, Northern Territory; CBG 8100854 with inflorescence, ex cultivation in Canberra; wild in running stream; Canberra live collection T31; Jiyer phenotype.

1980, June L. Craven; 13°04'S 132°24'E, near Barramundie Creek, 23 km southwest of Cooida, Kakadu National Park, Northern Territory; NSW 116; in black organic soil with shallow surface water, in swamp forest; the well-preserved herbarium specimen appears to be of the Jiyer phenotype.

1981 D. Levitt (1981) records taro for Groote Eylandt, Northern Territory, at Emerald River, and also occasionally in sandy areas behind beaches and in rocky areas. Aboriginal names for taro are also recorded.

1981 I. Crawford s.n.; 14°48'S 126°38'E, Ngerwaludalu, approximately 30 km from Kalumburu Mission, North Kimberley, Western Australia; WA, flowering specimen ex cultivation at Floreat Park; Aboriginal name, Ngerwal.

1981, September D. Harris and D. Yen; approximately 10 10'S 142°20'E, Moa Island, north of Saint Pauls, Moa Island, Cook District; CBG 8200958 with stolons; feral taro, used by islanders.

1981, 9 July N. White; map sheet Blue Mud Bay 1:100,000 AMG reference 570 020, Ngilipitji, Walker River, Parson's Range, northeast Arnhem Land, Northern Territory; La Trobe Botany Department voucher specimen NGW81-6; Canberra live collection number T338.

1981, December J. Purdie; Katherine Gorge National Park, Northern Territory; DNA 18972 with inflorescence.

1982, 11 November C. Dunlop and G. Wightman; 13°33'S 131°14'E, Black Jungle, Northern Territory; DNA 21004; aquatic in clayey loam creek line, in open area in rainforest.

1983, 18 August N. White; map sheet Blue Mud Bay 1:100,000 AMG reference 570020, Ngilipitji, Walker River, Parson's Range, northeast Arnhem Land, Northern Territory (same site as visited by White, 9 July 1981, above); Canberra live collection T331.

1983, 22 August N. White; collected by Ritharrngu person in Bawurrpanda (Annie Creek) area, map sheet Annie Creek 1:100,000 AMG reference c.880 500, northeast Arnhem land, Northern Territory; Canberra live collection T332.

1983, 27 August N. White; map sheet Annie Creek 1:100,000 AMG reference 840 455; Bawurrpanda (Annie Creek), northeast Arnhem Land, Northern Territory; Canberra

live collection T333.

1983, 27 September S. Brockwell (pers. comm. 1989); approximately 12°52'S 132°33'E, Kunkolomirrid Spring, upper South Alligator River, Northern Territory; photographic record; wild in permanent creek from spring, slightly above the adjacent floodplain, known to the local people but not eaten.

1984, 16 May S. Forbes; 17°11'20"S 128°15'E, altitude 360 m, Winnama Spring, 17.5 km south of Turkey Creek, Mabel Downs, southeast Kimberley, Western Australia; MEL 672191; abundant in organic humus, in permanent creek under shade of *Melaleuca leucadendra* and *Timonius timon*; Canberra live collection T337, Jiyer phenotype.

1984, 4 July K. Kineally; 17°15'S 128°26'E, 51.2 km southeast from Turkey Creek on track to Bungle Bungle outcamp, Kimberley, Western Australia; WA, field number 9188, with stolons; bulbous semiaquatic, stems rooting at nodes, extremely common in creek beds.

1984, 4 July S. Forbes; 17°13'S 128°24'30"E, altitude 350 m, tributary of Osmund Creek, 4.3 km northwest of Samim Mining Camp (at crossing of Swamp Creek) on Winnama Gorge-Bungle outcamp track, base of Osmund Range, southeast Kimberley, Western Australia; MEL 1534562; abundant in riparian forest with *Sesbania formosa*, *Pandanus ?spiralis*, *Cyclosorus interruptus*, on grey-black humus, rhizomatous, sterile population; Canberra live collection T334, ex. N. Scarlett collection NSA-1, Jiyer phenotype.

1984, 4 July N. Scarlett; 17°24'S 128°26'E, Wurlwurlji near Samim Mining Camp (at Swamp Creek crossing), 19 km due east of Osmund Valley Palms Yard, c. 26 km by mining track, on upper tributary of Osmund Creek, Osmund Range, southeast Kimberley, Western Australia; MEL 1533059; in dense patches in riparian forest dominated by *Syzygium angophoroides*, *Ficus coronulata*, *Nauclea orientalis*, and *Carallia brachiata*, associated with *Cyclosorus interruptus* (a second label also noted *Melaleuca leucadendra*, *Eucalyptus ptychocarpa*, *Heteropogon contortus*, *Ficus racemosa*, and *Eulalia fulva*); Canberra live collection T335, ex N. Scarlett collection NSB-2.

1984, 24 July S. Forbes; 15°37'S 126°23'E, 2.3 km east along nameless track off Kalumburu Road, 10 km north of Drysdale River Homestead, Western Australia, MEL, field number SJF 2715, see also Scarlett (1985); strongly rhizomatous, in mound spring with organic humus and free surface water, and with *Pandanus spiralis*, *Melaleuca viridis*, *Phragmites karka*, and *Cyclosorus interruptus*, surrounded by *Eucalyptus tedifica* dominated woodland; Canberra live collection T336, ex Melbourne Royal Botanic Gardens live collection 84–1455, Jiyer phenotype.

1985 R. Collins (pers. comm. 1985, describing undated collection pre-1985); Frenchman Creek near Babinda, northeast Queensland; Canberra live collection T263.

1985 R. Collins (pers. comm. 1985, field observation pre-1985); western side of Windsor Tableland, northeast Queensland; plants growing in a swampy gully.

1985, 11 September collector?; 13°10'S 134°52'E, Emu Springs, Arnhem Land, Northern Territory; DNA 0026510 (not sighted).

1985 H. Esler (pers. comm. 1986); c. 17°45'S 137°30'E, Malcolm Spring, upper Nicolson River, c. 100 km south of the Gulf of Carpentaria, Northern Territory; plants in

profusion in swamp created by small, artificial earth dam below the permanent spring, near foot of the China Wall; site possibly once a miners' camp.

1986 P. Latz; Blackfella Spring, upper Calvert River c. 100 km from the Gulf of Carpentaria, Northern Territory; plants scattered over several km downstream from permanent spring; Canberra live collection T376, Jiyer phenotype.

1986, 20 June G. Wightman (pers. comm. 1986); 1 km north of Cahill's Crossing, East Alligator River, Northern Territory; plants in moist loam, under monsoon vine forest.

1987 R. Tucker (pers. comm. 1987) reports pre-1987 observation of wild taro in upper Quintel Creek, 2 km upstream from the present Lockhart settlement, Cape York Peninsula, Queensland (the only site known to him in the vicinity of Lockhart), phenotype similar to wild taro common between Cooktown and Townsville (probably the Jiyer phenotype).

1987 G. Wightman (pers. comm. 1987) reports taro as rare on mainland, Northern Territory, but common on some offshore islands, Melville Island for example.

1987, 16 September P. Matthews; 18°53'S 146°13'E, Gap Creek intersection with Bruce Highway, Halifax Bay, northeast Queensland; abundant under remnant *Melaleuca leucadendra* scrub, below *Typha* swamp; field site 16/9/1, Jiyer phenotype.

1987 16 September P. Matthews; 18°52'S 146°10'E, Little Gin Creek intersection with Bruce Highway, Halifax Bay, northeast Queensland; field site 16/9/2, highly modified farm habitat, Jiyer phenotype.

1987, 20 September P. Matthews' 17°26'S 145°47'E, Jiyer Cave, Russell River, northeast Queensland; field site 20/9/1, plants abundant in permanent stream, firmly established by roots and stolons among rocks below waterfall off basalt cliff, alongside the Russell River, in rainforest, inflorescences emergent on some plants; type location for Jiyer phenotype; and for first Australian collection of *Tarophagus colocasiae*; *Alocasia* also present in drier situations than taro; Canberra live collection T395. Isolated clumps of taro with the Jiyer phenotype were also recorded on bends of the river within a few km below Jiyer Cave.

1987, 20 September T. Urvine; 17°26'S 145°47'E, approximately 1 km upstream from Jiyer Cave, upper Russell River, northeast Queensland; PJM field site 20/9/2, Jiyer phenotype; plants among rocks, in rainforest.

1987, 21 September P. Matthews; 17°27'S 145°50'E, Combo's Crossing, c. 5.7 km due east of Jiyer Cave, Russell River, northeast Queensland; plants abundant on open, muddy riverbank with grass, in rainforest; field site number 21/9/2, Jiyer phenotype.

1987, 25 September P. Matthews; 15°19'S 145°03'E, tributary of the Endeavour River, Hope Vale Mission road, first bridge after turnoff for Cape Flattery, Cape York Peninsula, Queensland; field site 25/9/2, Jiyer phenotype; plants in stream.

1987, 26 September P. Matthews; 15°17'S 145°06'E, upper tributary of Endeavour River, adjacent to the new Hope Vale Mission settlement, Cape York Peninsula, Queensland; field site 26/9/1, Jiyer phenotype; fruit green with seed (photo), plants abundant over 500 m in permanent stream above river, in riparian rainforest with *Alocasia*, *Pandanus*, *Dillenia*, *Ficus*, *Livistona* and *Entada*; the taro is regarded by local residents as inedible and is known to have been present since at least the 1930s, before

the mission settlement was built; Canberra live collection T394.

1987, 29 September P. Matthews; 16°22'S 145°20'E, upper tributary of Whyanbeel Creek, northeast Queensland (access courtesy Alan Carle); CBG 88071984; field site 29/9/1, Jiyer phenotype; plants in steep, rocky stream in rainforest.

1987, 29 September P. Matthews; 16°19'S 145°19'E, Stewart Creek, tributary of Daintree River, northeast Queensland; field site 29/9/87, Jiyer phenotype; isolated clumps on both sides of creek, just above ford, with remnant rainforest.

1987, 30 September P. Matthews; 16°18'S 145°19'E, Cassowary Creek, c. 200 m upstream from Stewart Creek road, on creek banks in deforested farmland; site 30/9/1, Jiyer phenotype.

1987, 30 September P. Matthews; 16°29'S 145°24'E, South Mossman River at intersection with Cook Highway, abundant in dense patch of soft bank of accumulated detritus, under remnant of riparian broadleaf rainforest, surrounded by sugarcane fields; field site 30/9/2, Jiyer phenotype, flowering.

1987, 1 October P. Matthews; 17°15'10"S 145°55'51"E, Harvey Creek, 1 km east of the new Bruce Highway, permanent tributary of Mulgrave River, northeast Queensland; field site 1/10/1, Jiyer phenotype; in creek bank at downstream end of a long island, at edge of rainforest remnant.

1987, 1 October P. Matthews; 17°10'0"S 145°49'42"E, western flank of Behana Gorge, in first stream after the Cairns-Mulgrave water pumping station, above road, tributary of Behana Creek and Mulgrave River, northeast Queensland; field site 1/10/2, Jiyer phenotype; in thin rainforest with *Pandanus*, distributed upstream to at least 20 m distance, out of view of the road.

1987, 2 October P. Matthews; 17°20'S 145°52'E, Boulder Falls, North Babinda Creek, tributary of Russell River, northeast Queensland; field site 2/10/1, Jiyer phenotype clump at base of major waterfall and also in isolated small clumps along both sides of creek above the waterfall, in rainforest.

1987, 2 October P. Matthews; 17°32'S 145°50'E, upper tributary of Badgery Creek, both sides of forestry road bridge, Borong State Forest, above north Johnstone River, northeast Queensland; CBG 8807195; field site 2/10/2, Jiyer phenotype, though with unusual tendency to form asymmetric leaf blades; abundant over 200 m of open, rocky stream bed in rainforest, flowering.

1987, 3 October P. Matthews; 18°34'S 146°14'E, Blue's Patch, lower Seymour River, above Neam Inlet (property of B. Costa), Ingham district, lower Herbert River, northeast Queensland; field site 3/10/1, Jiyer phenotype; a few large plants overcrowded by *Panicum grass* invasion, in remnant stand of *Melaleuca*, on sugarcane farm. This patch was known locally to have been present for at least 55 years, and other taro patches were known in this area before the almost complete clearance and drainage of the *Melaleuca* swamp forest.

1988 D. Rentz; 17°15'S 145°38'E, Lake Barrine, Atherton Tableland, northeast Queensland; by edge of lake, in rainforest at least 15 m from walking track, c. 250 m from tourist centre; Canberra live collection T398, Jiyer phenotype.

1988, June N. Williams; 17°13'S 128°14'E, a few km south of Winnama Spring,

upper Turkey Creek, southeast Kimberley, Western Australia; below a permanent spring, *Pandanus* and *Livistona* present, site located by Aboriginal informants; Canberra live collection T386, Jiyer phenotype.

1989 Alan Burwood Calendars (1989), 1989 calendar with clearly distinguishable taro visible at base of Milaa Milaa Falls, upper tributary of north Johnstone River, northeast Queensland; photo by F. Prenzel (pers. comm. 1989).

1989, 6 March R. Hinxman (pers. comm. 1989); 17°10'56"S 145 50'01"E, eastern flank of Behana Gorge, base of Barnard's Spur, tributary of Behana Creek; Jiyer phenotype, plants abundant at each end of a 400 m long anabranch in creek, among granite boulders, in rainforest; at least one hundred inflorescences visible in a single view of the taro patch, fruit green with nearly mature seed (photo), and colonised by larvae of an unidentified species of Syrphidae (hover fly).

1989, 7 October R. Hinxman (pers. comm. 1989); 17°26'30"S 145 46'30"E, Tewon Creek, tributary of Russell River, northeast Queensland; Jiyer phenotype, in rainforest: no fruits or flowers; Canberra live collection T397.

1989, 8 October R. Hinxman (pers. comm. 1989); Moochoopa Falls, on nameless tributary (not on Moochoopa Creek, mislabelled on Bartle Frere Sheet 8063), 2 km due north of Jiyer Cave, above the Russell River, northeast Queensland; Jiyer phenotype, at base of waterfall in rainforest; no fruits or flowers; Canberra live collection T396.

Appendix 18. R. Tucker correspondence

Mr Robert Tucker, a gardener/curator at Rockhampton Botanical Gardens, kindly sent me the following letters based on his experiences in northern Queensland.

1st June, 1987.

Dear Peter,

Thank you for your interesting letter and research proposal involving Taro. Both wild and cultivated Taros have interested me for many years and I have made numerous live collections and maintain these plants in several localities.

Wild Taro occurs very infrequently on the northern Cape York Peninsula, although the Aboriginals at Lockhart River have memories of its uses as food. The wild plants are now quite uncommon due to predation by feral pigs, but those that I saw in the Lockhart area were vegetatively identical to the plants common in the Cooktown to Townsville region. They are green, stoloniferous plants which produce viable seeds and in cultivation are interfertile with diploid cultivars, as my own pollination studies have shown.

In my opinion, it would be very difficult to collect wild plants in the Lockhart area. The only site I know which had these plants was along upper Quintel Creek about 2 kms. upstream from the village. However wild taro in creek habitats are rather temporary. The old people in the village say there used to be a large swamp near the "Old Site" eg. the previous Lockhart River village, where presumably wild taro grew. The Lockhart people do not cultivate garden taro, even though it has been introduced to the area by various people, including myself.

I lived at Lockhart on three field trips, the last stay was for twelve months and I have an extensive knowledge of the region and its vegetation.

I assisted Sonya Plompen in her collection of wild taro in the Cairns area and have observed these plants in great numbers between Cooktown and Townsville. They are all identical. The Lockhart plants are similar (we have some growing here!) but are probably next to impossible to relocate. The most interesting feature of the wild taros is their lack of pigmentation, so when I occasionally find an identical plant with pigmented petioles etc. I take notice. In the Bamaga area, Atherton Tablelands and Tweed Heads areas are plants which are essentially similar to the usual wild taro, but have blackish petioles. I have plants here of a New Guinean cultivar which is very similar and which flower regularly. They seem to be very widespread.

There are currently about thirty (30) taro cultivars in north Queensland, none of which persist in the wild in my experience, except possibly some of the stoloniferous fertile forms.

I believe that the wild taros are truly native and are not introduced. In most areas the Aboriginals did not use them, and in those few places where they were used, the parts used and methods for preparation were purely Aboriginal and did not reflect any technologies used in taro cultivation areas like New Guinea. For example, the Aboriginals in Queensland did not eat taro leaves, which is a common practice in places where taro cultivation is established. One would assume that some information on the food value of the leaves would have been passed on to the Aboriginals if the plant had been introduced to them from elsewhere. Instead they treat the corms in the same way as toxic yams and *Amorphophallus* corms, cooking, grinding, soaking and cooking them again to remove the calcium oxalate. I also find it hard to understand why any taro cultivating people would distribute the scarcely edible stoloniferous forms when superior cultivars were available.

Wild taro also belongs to a floristic community that is widespread in South-East Asia, Melanesia and Australia and could have arrived here by natural means during any period prior to humans. Its habitat associates occur over a wide area and some of them, particularly the fern *Stenochlaena palustris* (which occurs up to Malaysia at least) are less mobile, not being moved by birds as taros are. So I really see no reason to consider wild taros as not native.

I think taro researchers have overlooked New Guinea as the source of cultivated forms. It now seems obvious that taro cultivation, probably involving selected tetraploids as well as selected diploids has been established in New Guinea for perhaps as long as 10,000 years. New Guinea has by far the greatest array of cultivars. The number of cultivars in any region diminishes to the west and to the east, whilst this reduction in variety is quite evident, it is also obvious that the cultivars become more removed from the wild form the further one goes from New Guinea. If New Guinea is the origin of cultivated taros, and remember Australia has been connected to New Guinea several times, it seems perfectly logical to assume that parental forms occurred here naturally as well.

In Queensland there is further evidence of the indigenous nature of wild taro in the

array of insects and birds that are adapted to it as a food resource. Taro cultivation is made difficult in high rainfall areas because of some of these.

I hope all this is some help in your studies.

30th October, 1987.

Dear Peter,

I am sorry to have missed you when you came up this way. As it turns out you appear to have had a worthwhile trip.

Regarding an Aboriginal name for any taro clone, I feel it is perhaps useless to select a name from one language and apply that to the broader range of related plants. There were probably over 20 languages, that included in their vocabulary, terms for Taro plants, the cooked product or parts thereof. Also you really have no way of knowing if a particular name belongs with the Taros in that area today, despite my assertion that all the wild Taros in north Queensland are essentially the same.

Wild Taros are opportunistic plants and normally are colonisers of (favourably) altered sites, usually washouts, flood debris banks, deposition sites inside meanders and the like. Such habitats are usually temporary and it is my experience that large colonies (of many hundreds of plants) can form in less than 12 months on favourable sites, give a deceptive appearance of age. Now we have cleared farmlands etc. which allow longterm colonisation, due to greater stability of the environment. Other long-term habitats include swamp forest and (volcanic) lake margins, where, presumably they are spread by migrating waterfowl or some other movement. The crater lakes of Eacham and Barrine have wild Taros at an elevation of near 1,000 m. Elsewhere they are rare at high elevations, but due more to a lack of habitat than to temperature.

I still have some plants of the Lockhart Taro, in fact we have just planted a collection of wild and cultivated Taros here in which the Lockhart clone was included. We can send you some when we have propagated it. The Lockhart plants are essentially like those from the Cooktown to Townsville area.

That Queensland Aborigines did not eat Taro leaves, is my own experience from both observation and questioning. Nor have I ever heard or read of their using the leaves as food from any other source.

In preparation, the Cape York Peninsula Aborigines that I know, used a technique that is also used on toxic *Dioscorea* and *Amorphophallus* corms:

1. Bake corms (whole) in amai (earth and stone oven) wrapped or unwrapped.
2. Peel cooked corms.
3. Pound cooled corms into paste, something like Polynesian "Poi".
4. Place paste in very fine "punya" - (a bag made of *Lomandra* leaf fibres) and soak in *running* water for at least one day. Up to 20 "punyas" may be tied in a bunch and soaked in this fashion.
5. Soaked paste ("mai-i") is drained of excess water, usually by hanging in a tree.
6. Drained paste is fashioned into (1) cakes or balls and "dryfried" on a hot rock in the centre of the fire; (2) cylinders rolled in leaves or bark and baked in hot sand, ashes

or in an amai; (3) rolled into balls and boiled in a pot (traditionally an “alup” - bailer shell) in coconut milk or turtle stew to make a rich sauce-like soup. The term “mai-i” refers to any edible vegetable matter and is used over most of northern Cape York Peninsula. The coconut milk and bailer-shell technology comes from Torres Strait and therefore probably from New Guinea.

This information was obtained from Aborigines that I lived with for over a year, but who no longer practised wild Taro harvesting. I did observe other corms (*Amorphophallus*, *Dioscorea* etc.) being treated in this way. Also “wunki” (*Rhaphidophora pinnata*) stems are cooked in this way.

All the Aborigines and Islanders I know have no traditional use of Taro leaves or cultivated *any* forms at all, with the exception of the extreme eastern and northern Islands (Saibai, Boigu, Erub, Mer etc.) who were more Papuan.

Whilst in Hawai'i, I visited several Arboreta and collections that housed collections of Hawai'ian taro cultivators. Most of them are smallish plants, grown in running water and bear strong similarities to old New Guinean clones. Many are fertile and most are somewhat stoloniferous. Honolulu Botanic Gardens is going to send us a collection of them.

Appendix 19. Frequently used stock solutions

Frequently used stock solutions, in order of first appearance in Chapter Ten (Materials and Methods). Many of these stocks are described by Maniatus et al. (1982), or other standard laboratory manuals. The solutions can be stored for indefinitely long periods unless otherwise stated.

(1) **Leaf DNA extraction buffer:** 50 mM Tris.HCl pH 7.5, 200 mM Na₂EDTA, 100 mM NaCl. Autoclave and store at room temperature (RT).

(2) **Ethanol perchlorate solution (EPR):** Sodium perchlorate (NaClO₄. H₂O) in 80% ethanol, prepared as follows. Dissolve 40 g NaClO₄. H₂O in ethanol, to a volume of 320 ml; dissolve 120 g NaClO₄. H₂O in H₂O to a volume of 80 ml; combine the solutions and store the mixture in a brown glass bottle at RT.

(3) **50 TE 20(8):** 50 mM Tris and 20 mM Na₂EDTA, pH 8.0, prepared from a 50x stock for which the final pH was adjusted to 8.0 with HCl or NaOH. Store 1x stock at RT, 50x stock at 4°C.

(4) **Phenol:** To prepare phenol saturated with aqueous buffer, dissolve high quality crystalline phenol in a glass container, placed in hot tap water. Extract the melted phenol repeatedly by shaking it with 1 M Tris.HCl pH 8.0, until the pH of the discarded aqueous phase is more than 7.6 according to a litmus paper test. Finally, extract once with 0.1 M Tris.HCl pH 8.0, or with distilled H₂O. Store in brown glass bottle at 4°C or -20°C for up to several months. Aliquot small amounts for storage and use at RT. After long

storage, phenol turns pink because of oxidation, and the solution should be discarded before oxidation turns the solution red.

(5) **Chloroform**: Mix chloroform with isoamyl alcohol in the ratio 24:1. Store in brown glass bottle at RT.

(6) **Ethanol and sodium acetate**: Prepare 2 M sodium acetate, pH 5.5, by dissolving 27.2 g sodium acetate with 3H₂O in 80 ml H₂O, adjust pH to 5.5 with glacial acetic acid, then take volume to 100 ml with H₂O. Mix 5 ml of this solution with 95 ml of 100% ethanol. Store at RT. To precipitate DNA from aqueous solutions with very little or no salt, add two volumes of the ethanol and sodium acetate mixture. This gives a final concentration of 67 mM sodium acetate and 63% ethanol.

(7) **10 TE 1(8)**: 10 mM Tris and 1 mM Na₂EDTA, pH 8.0, prepared from a 100x stock for which the final pH was adjusted to 8.0 with HCl or NaOH. Store 1x stock at RT, 100x stock at 4°C.

(8) **Boiled RNA'se A (pancreatic RNA'se)**: Dissolve 10 mg per ml in a solution of 10 mM Tris.HCl pH 7.5, and 15 mM NaCl. Boil at 100°C for 15 minutes, let cool slowly to RT, then dispense into aliquots. The stock is good for at least several months if stored at -20°C.

(9) **GET buffer**: 50 mM glucose, 10 mM Na₂EDTA, 25 mM Tris base, final pH 8.0. Dissolve 0.9 g glucose, 0.3 g Tris, and 0.37 g Na₂EDTA in H₂O, adjust pH to 8.0, and add H₂O to a final volume of 100ml. Store at 4°C.

(10) **3 M potassium, 5 M acetate**: To 60 ml of 5 M potassium acetate, add 11.5 ml of glacial acetic acid and 28.5 ml of H₂O. The pH is approximately 4.8. Store at RT.

(11) **Luria-Bertani (LB) medium**: From Maniatus et al. (1982), with modification. Glucose and magnesium chloride are optional. Add 10 g Bacto-tryptone, 5 g Bacto-yeast extract, 5 g NaCl, 2 g glucose, and 0.2 g MgCl₂ to one litre of H₂O. Mix well and autoclave. Store at RT. Omit MgCl₂ when using the medium with tetracycline.

(12) **5 M NaOH**: Store at RT.

(13) **10% sodium dodecyl/ sulphate (SDS)**: Store at RT.

(14) **Ethidium bromide**: Prepare 10 mg/ml stock by dissolving 0.2 g ethidium bromide powder in 20 ml H₂O. Stir with magnetic stirrer for several hours, then wrap container in aluminium foil, or transfer to dark bottle. Store at 4°C. The pH can be adjusted to make the powder more soluble. Carcinogen.

(15) **Restriction enzyme buffers:** Initially, the low, medium, and high salt buffers recommended by Maniatus et al. (1982) were used. For much of the later work, the all-purpose TA buffer (O'Farrell et al. 1980) was found equally reliable and more convenient. All the buffers were stored at -20°C . 15.1 **10x low-salt buffer:** 100 mM Tris.HCl pH 7.5, 100 mM MgCl_2 , 10 mM dithiothreitol (DTT). 15.2 **10x medium-salt buffer:** 0.5 M NaCl, 100 mM Tris.HCl pH 7.5, 100 mM MgCl_2 , 10 mM DTT. 15.3 **10x high-salt buffer:** 1 M NaCl, 0.5 M Tris.HCl pH 7.5, 100 mM MgCl_2 , 10 mM DTT. 15.4 **Tris.acetate (TA) buffer:** The final 1x reaction concentrations are 33 mM Tris.acetate, 66 mM potassium acetate, 10 mM magnesium acetate, 0.5 mM dithiothreitol, 100 $\mu\text{g}/\text{ml}$ bovine serum albumin (BSA), and pH 7.9. To make 10x stock, prepare three solutions: (A) 0.41 M Tris.acetate, 0.83 M potassium acetate, 0.12 M magnesium acetate, adjusted to pH 7.9 with glacial acetic acid; (B) 50 mM DTT; (C) 10 mg BSA/ml H_2O . Mix A:B:C: in ratios 8:1:1.

(16) **Bromophenol blue (BPB) running dye:** For 2 ml of stock, mix 0.4 ml of 0.5M Na_2EDTA pH 8.0, 1.5 ml glycerol, 0.1ml of 1 M Tris.HCl pH 7.8, and 1 mg of BPB powder. Store aliquots at 20°C for long periods, and at RT for current use. Add 3–6 μl per 50 μl reaction mixture.

(17) **Tris.acetate electrophoresis (TAE) buffer:** The 1x solution contains 40 mM Tris.acetate, 1 mM Na_2EDTA . To prepare 50x stock, dissolve 242 g Tris base in H_2O , add 57.1 ml glacial acetic acid, 100 ml 0.5 M Na_2EDTA pH 8.0, and H_2O to a volume of 1 litre. Do not autoclave, store at 4°C . The 1x solution may be reused for electrophoresis at least four times, with remixing, but excessive reuse may contaminate gels and filters with DNA.

(18) **Denaturing solution:** 0.5 M NaCl, 0.5 M NaOH. Store at RT.

(19) **20x Standard saline citrate (SSC):** Dissolve 175.3 g NaCl and 88.2 g sodium citrate ($\text{Na}_2\text{H}_2\text{H}_2\text{O}$) in 800 ml H_2O . Adjust pH to 7.0, and make up to 1 litre. Autoclaving optional, store at RT.

(20) **100x Denhardt's:** Dissolve 2 g Ficoll 400, 2 g polyvinyl-pyrrolidone (PVP, MW 360,000), and 2 g bovine serum albumin in H_2O to a volume of 100 ml. Store 10 ml aliquots at 20°C .

(21) **Pre-hybridisation solution:** Mix 4 ml of 10% SDS, 60 ml of 20x SSC, 20 ml of 100x Denhardt's, and 200 ml formamide (Fluka-purum) with 10 TE 1(8) to a volume of 400 ml. Final concentrations: 0.1% SDS, 3x SSC, 5x Denhardt's, 50% formamide, 3 mM Tris. HCl, and 0.3 mM Na_2EDTA . Store at -20°C .

(22) **5x ligase buffer:** 0.25 M Tris.HCl pH 7.8, 50 mM MgCl_2 , 250 $\mu\text{g}/\text{ml}$ bovine serum albumin. Store at -20°C .

(23) **Neutralising solution:** 3 M NaCl, 0.5 M Tris base, (2 M NaCl 0.5 M Tris, may also be used). Store at RT.

(24) **10x Calf intestine phosphatase (CIP) buffer:** 0.5 M Tris.HCl pH 9.0, 10 mM MgCl₂, 1 mM ZnCl₂. Store at -20°C.

(25) **0.2% w/v colchicine:** Dissolve 20 mg colchicine in 10 ml H₂O. Aliquots can be stored at -20°C for at least several months.

(26) **5x RNA polymerase buffer:** 40 mM Tris.HCl pH 7.9, 10 mM MgCl₂, 0.1 mM Na₂EDTA, 150 mM KCl, 50% w/v bovine serum albumin. Store at -20°C.

Appendix 20. General survey of rDNA variation in taro

Summary of tests for the general survey of rDNA variation in *C. esculenta* (L.) Schott, not including var. *fontanesii*. Restriction enzyme digestion by *Taq* I and *Hinf* I was followed by analysis with probes made from either the cloned rDNA fragment in pCe34.1 (the 5.5 kb *Eco* RI fragment), or the 2.8 kbp *Taq* I large-intergenic-spacer fragment, from subclone pCe34.11 or excised directly from pCe34.1.

Ribosomal DNA classes, defined on the basis of *Taq* I and *Hinf* I spacer fragments, are recorded. Tests with *Taq* I and *Hinf* I did not always allow a determination of rDNA class, when tests were run on separate gels for example, or when autoradiographs were faint and not all fragments could be detected. In the circumstances just outlined, independent estimates of fragments could nevertheless be made, and these contributed positively to the summary statistics presented in Chapter Fourteen.

Chromosome counts (2n), for one plant per site, were made by P. J. Matthews (no asterisk), P. Gaffey (one asterisk), and T. Kawahara (two asterisks). The habitat, cultivated or wild, is indicated for each sample.

Australia

ANU T#	Location	Eco 5.5kb		Taq 2.8kb		rDNA class	2n=	Hab.
		Taq	Hinf	Taq	Hinf			
31	Arnhem Land	X	X	X	X	Arn 2:2		WILD
33	Queensland						28*	WILD
331	Arnhem Land	X		X	X	Arn 2:2		WILD
332	Arnhem Land	X						WILD
333	Arnhem Land			X	X	Arn 2:2		WILD
334	Kimberley						28	WILD
335	Kimberley			X	X	Kim 2:2	28	WILD
336	Kimberley	X	X	X	X	Kim 2:2		WILD
337	Kimberley	X						WILD
338	Arnhem Land	X						WILD
376	Carpentaria	X	X	X	X	Arn 2:2	28	WILD
386	Kimberley			X	X	Kim 2:2		WILD

Queensland Sites (1987 field trip)

1	Whyanbeel Ck	X	X			Qld 1:1		WILD
2	Harvey's Ck	X	X			Qld 1:1		WILD
3	Combo's X'ng	X	X			Qld 1:1		WILD
4	Badgery Ck	X	X			Qld 1:1		WILD
5	Hope Vale	X					28	WILD
6	Cassowary Ck	X						WILD
7	Sth Mossman R.	X						WILD
8	Blue's Patch	X					28	WILD
9	Boulder Falls	X						WILD
10	Jiyer Cave	X	X	X	X	Qld 1:1	28	WILD
11	Gap Ck	X						WILD
12	Gin Ck	X						WILD
13	L. Barrine			X	X	Qld 1:1		WILD

Note: In the Queensland survey, 35 plants were tested with Taq I and 14 with Hinf I.

Papua New Guinea

1	WH	X	X			Puk 2:3	28*	CULT
11	EH	X					28*	CULT
19	ENB			X	X		28*	CULT
21	Moresby	X	X					WILD
23	Moresby	X					28*	CULT
46	WH	X	X					CULT
49	WH	X	X				28*	CULT
50	WH	X						CULT
112	Solomon Is.	X	X					CULT
160	WH	X	X			Ruti 3:2B		CULT
163	WH	X	X			Puk 1:2		CULT
164	WH	X	X			Ruti 3:2A		CULT
166	WH	X	X			Qld 1:1		CULT
167	WH	X	X			Puk 2:3		WILD
171	WH	X						CULT
172	WH	X	X			Qld 1:1		CULT

178	WH	X	X			Puk 2:3		CULT
179	WH			X	X			CULT
182	WH	X	X			Puk 1:2		CULT
183	WH	X	X			Puk 1:2		CULT
184	WH				X			CULT
186	WH	X	X			Puk 1:2		CULT
187	WH	X	X			Puk 2:3		CULT
188	WH	X	X			Puk 2:3		CULT
190	WH	X	X			Puk 2:3		CULT
193	WH	X	X			Puk 2:3		CULT
197	WH	X	X			Puk 1:2		CULT
198	WH	X	X			Puk 1:2		CULT
200	WH				X			CULT
202	WH	X	X	X	X	Puk 1:2		CULT
203	WH	X	X	X	X	Buk 2:1		CULT
205	WH	X	X			Puk 1:2		CULT
206	WH	X	X					CULT
207	WH	X						CULT
208	WH	X	X			Puk 1:2		CULT
209	WH	X	X			Puk 1:2		CULT
211	WH	X	X			Puk 1:2		CULT
212	WH	X						CULT
213	WH	X						CULT
225	Morobe	X	X	X	X	Moro 2:2		WILD
226	Morobe	X	X	X	X	Moro 2:3A		WILD
227	Morobe	X	X	X	X	Moro 2:3B		WILD
228	Morobe	X	X	X	X	Puk 1:2		CULT
229	Morobe	X	X	X	X	Moro 3:3	28	CULT
231	Morobe	X						CULT
234	Morobe	X	X	X	X	Puk 1:2		CULT
235	E. Sepik	X	X			Puk 1:2		CULT
236	E. Sepik	X	X			Puk 1:2		CULT
237	E. Sepik	X	X			Puk 1:2		CULT
238	E. Sepik	X	X					CULT
239	E. Sepik	X	X			Ruti 3:2B		CULT
240	E. Sepik	X	X			Puk 1:2		CULT
242	E. Sepik	X	X			Puk 1:2		CULT
243	?	X	X					CULT
247	ENB	X	X			Qld 1:1		CULT
249	WNB			X	X			CULT
251	?	X						CULT
256	Morobe		X					CULT
258	E. Sepik	X	X			Qld 1:1		CULT
259	WH	X	X					CULT
348	Solomon Is.	X	X					CULT

WH = Western Highlands Province; EH = Eastern Highland Province; ENB = East New Britain Province; E. Sepik = East Sepik Province; Morobe = Morobe Province; ? = unprovenanced within PNG

Asia and Madagascar

107	Philippines			X	X		28*	CULT
109	Timor	X	X				28*	CULT
110	Timor	X	X				42*	CULT
131	Philippines	X	X	X	X	Puk 2:3		CULT
134	Philippines	X	X			Bay 2:2		CULT
137	Philippines	X	X					CULT
139	Philippines	X	X					CULT
140	Philippines	X	X					CULT
141	Philippines		X					CULT
142	Philippines	X	X					CULT
143	Philippines			X	X			CULT
152	Philippines	X						CULT
155	Philippines	X	X					CULT
156	Philippines			X	X	Bay 2:2		CULT
293		X	X				42*	CULT
294		X	X				42*	CULT
295	Japan	X	X			Min 3:2		CULT
296		X	X					CULT
297	Japan	X	X					CULT
298	Japan	X	X					CULT
299		X	X				42*	CULT
302		X	X				42*	WILD
303	Japan	X	X					CULT
304		X	X					CULT
305	Japan	X	X					CU LT
306	Japan	X	X					CULT
309	Nepal			X	X	Kat 2:3	42*	CULT
310	Nepal			X	X	Kat 4:4	42*	CULT
319	Sri Lanka			X	X			WILD
320	Sri Lanka			X	X	Col 2:2		WILD
323	Sri Lanka			X	X	Col 3:4		WILD
326	Japan	X	X					CULT
327	Japan	X	X			Col 3:4		CULT
340		X	X			Min 3:2		CULT
355	Thailand		X				28*	CULT
359	Thailand		X					CULT
363	Madagascar	X	X			Puk 2:3		CULT
364	Madagascar	X	X			Col 3:4		CULT
365	Madagascar	X	X			Col 3:4		CULT
366	Madagascar	X	X			Puk 2:3		CULT

Pacific Island

104	Hawai'i	X	X	X	X	Old 1:1	28*	CULT
106	Hawai'i	X	X	X	X	Puk 1:2		CULT
114	Easter Is.		X	X	X			CULT
117	Easter Is.			X	X	East 1:3	28*	CULT

119	Easter Is.			X	X	East 1:3		CULT
124	Huahine Is.	X	X	X	X	Puk 2:3	28*	CULT
126	Huahine Is.	X	X			Qld 1:1		CULT
127	Huahine Is.	X	X			Qld 1:1	28*	CULT
272	Aotearoa	X					42	WILD
274	Aotearoa	X					42	WILD
275	Aotearoa	X						WILD
276	Aotearoa	X					42	CULT
277	Aotearoa	X					42	WILD
278	Aotearoa	X					42	CULT
279	Aotearoa	X					42	CULT
282	Aotearoa	X					42	CULT
283	Aotearoa	X					42	CULT
284	Aotearoa	X					42	WILD
286	Aotearoa	X					42	WILD
287	Aotearoa	X					42	WILD

Appendix 21. Sampling protocol for wild taro survey

The following protocol was prepared before the first survey of wild taro in Queensland, Australia, in 1987. At that time, leaf samples for DNA analysis had be preserved in liquid nitrogen in order to obtain sufficient quantities of high quality DNA for restriction enzyme analysis. Today, when collecting leaf samples for studies that make use of the Polymerase Chain Reaction (PCR), the quantity and quality of DNA needed is much less. In the field, all that is needed are about 8 g of young leaf tissue, stripped out from between the major veins of the blade and placed in a sealed plastic zip bag with a few grammes of dry silica gel. It is important not to add too much leaf, relative to the amount of silica, because the aim is to dry the leaf tissue as quickly and thoroughly as possible. After quick drying, the tissue will keep its green colour, and provide a good yield of DNA using any standard extraction method. To prevent the tissue from breaking into fragments after dessication, it should be spread out between two pieces of filter paper (or inside a coffee filter envelope) when first put in the bag with silica. With this method of tissue collection, it is easy to quickly sample many plants from within one site, or from many sites in one day. If three bags are prepared from one morphotype or taro variety at one site, I label the bags as 1/3, 2/3, 3/3 if each bag represents a separate leaf from a separate plant. If the samples are strict replicates from a single plant, then the bags are labelled 1a/3, 1b/3, 1c/3 etc. In both cases, the first number indicates what kind of sample was made (a strict replicate, or from separate plants), while the second number indicates how many samples were collected. In 1987, the following protocol for collecting samples was used with minor modifications in the field, but was not included in the 1990 thesis. A field guide for describing and recording wild taro and wild taro sites was published later (Matthews 1997; see Appendix 22 this volume), and can be read as a

complementary text.

General aim and method

Looking for evidence of a homogeneous and generally dispersed taro population, distinct from recently introduced cultivars. First priority will be given to isolated, wild patches, large or small. The second aim is to look for evidence of sexual reproduction in the area and to sample in such a way that it can be demonstrated. In large and isolated wild sites, representative sampling will be attempted on an approximate grid system (approximation dependent on terrain) and using relatively large samples. Such samples will be of use in both measuring the effects of sexual reproduction in a local population and in measuring the homogeneity in what may be part of the historically important, regional population. For contrast to these samples, spot samples will be taken of locally grown cultivars and roadside-wild patches to see what types are present and whether they have any relationship with the putative isolated-wild populations. If large, isolated populations are lacking, then not-isolated large, wild populations (e.g., roadside) will be sampled in a representative fashion in order to provide at least the sought-for measure of local, sexual reproduction. In all situations, whatever the desired sample size, the sample number will be achieved by first sampling between clumps, and if this is not possible, then between shoots within a clump.

Cultivated varieties/locally grown market specimens

These may include varieties which are also found in roadside-wild sites. Since they are being moved around the local area, both the cult and feral plants may have interbred with whatever remains (if anything) of pre-European populations. A double frozen-leaf sample or a single live-sample of these will be collected, preferably the former to reduce later maintenance effort. If possible, leaf measurements, flower measurements, and general-phenotype records will be made. Such observations will be made on no more than three each of leaves, flowers, and shoots; a number of one is enough if time is limited.

Roadside — wild

Large patches (clumps dispersed over several metres, for example) may represent a small, sexually reproducing population of ramets. Some priority will be given to those with evidence of flowering, over those without. From such large patches, three samples of live shoots will be taken from those positions which seem least likely to represent branches of a single ramet. If possible, a further six frozen leaf samples will be taken, but only from separate clumps from which live shoots haven't been taken. Phenotypic observations will be made of the shoots from which each "N" and "L" sample, and further phenotypic observations will be made for up to twelve leaves or shoots. With larger roadside populations, for instance where clumps are dispersed over hundreds of metres along a valley, more sampling may be considered. This will depend on time limitations and the extent to which sampling aims for isolated-wild sites have been satisfied. For very small roadside sites, one live sample and/or three frozen samples is sufficient, along with phenotypic observations of up to three leaves/flowers, and general-phenotypic of one

shoot if the patch or clump is of apparently uniform phenotype.

Isolated — wild

Ideally, large samples of 40–60 could be obtained from large patches where sexual reproduction occurs, in three separate populations in the survey area. This sample size would be achieved with N and L collections in the ratio of 2:1 and represents the largest manageable number of samples. If suitable leaves for freezing are unavailable, more live samples will be taken (relative to frozen) to make up the desired number. If the population is smaller than 60 clumps, it will be sampled completely with an N:L sample ratio of 2:1. Where the population is widely and loosely scattered, and numbers (in terms of clumps) much more than 60, no more than 40 shoots representing clumps will be collected, and up to 40 frozen samples will be made, if possible.

Appendix 22. Field guide for wild-type taro, *C. esculenta* (L.) Schott

Original publication: Matthews, P. J. (1997) Field guide for wild-type taro, *Colocasia esculenta* (L.) Schott. *Plant Genetic Resources Newsletter* 110: 41–8.

Summary

This guide is designed to encourage research on wild and possibly natural varieties of taro (wild-types). A short form is provided for recording one plant in one site. With practice, this form can be completed in 10 minutes. The form can also be used to record cultivated varieties of taro, but is not intended as a substitute for the longer FAO descriptor list.

Resume

Guide de terrain pour les types sauvages de taro, *Colocasia esculenta* (L.) Schott

Ce guide a pour but d'encourager la recherche sur les varietes sauvages et eventuellement naturelles de taro (types sauvages). Un formulaire abrege est fourni pour renregistrement d'une plante dans un site donne. Avec un peu de pratique, ce formulaire peut etre rempli en 10 minutes. Il peut aussi etre utilise pour enregistrer les varietes cultivees de taro, mais il n'est pas destine a remplacer la liste plus complete de descripteurs de la FAO.

Resumen

Guia de campo para la malanga o taro silvestre, *Colocasia esculenta* (L.) Schott

Esta guia tiene como objetivo estimular la investigacion de variedades silvestres y posiblemente naturales de la malanga o taro (tipos silvestres). Se facilita un breve formulario para registrar una planta en un dado sitio. Con la practica, dicho formulario podra rellenarse en 10 minutos. Tambien podra servir para registrar variedades cultivadas de malanga o taro, aunque no se pretende que substituya a la lista de descriptores de la FAO, que es mas larga.

Introduction

Before the last two centuries of rapid and international plant dispersal, taro was possibly the world's most widely distributed staple crop, ranging from India and Southeast Asia to Northeast Asia, the Pacific Islands, Madagascar, Africa and the Mediterranean (Matthews 1995). Taro can be regarded as a major crop that is minor in many places. Production from 1962 to 1975 apparently rose from 3.3 to 4.5 million metric tonnes, but the estimates were not considered reliable (Wang 1983). A figure of some 400 million users of taro (Bown 1988) or root crops (Wang 1983) is commonly cited, but this figure clearly does not include the huge number of people who use taro in subtropical and fully temperate regions of East Asia. As with many minor crops, or apparently minor crops, research on taro has been very limited (Matthews and Terauchi 1994).

To help investigators recognize and record different taro varieties, the form presented in this guide has two main sections, one for vegetative traits, and the other for floral traits and development. For scientific and/ or practical purposes, we need to learn much more about reproduction by wild and cultivated taros. In most situations, cultivated taros are propagated vegetatively, and sexual reproduction is prevented by a loss of flowering ability (Duncan et al. 1985), or because harvesting takes place before flowers or seed develop, or because cultivation takes place in an area with unsuitable climate or no pollinators. For cultivated taros, the most likely opportunities for breeding are when plants escape from cultivation, or are left unharvested in neglected or fallow fields, or when some cultivated plants do reach maturity and release pollen that is then carried by insects to nearby wild taros. For wild taros in tropical Papua New Guinea, there is ample evidence that breeding takes place (Barrau 1959; Carson and Okada 1980; Ivancic et al. 1995).

In theory, wild-type taros may exist in (i) wild, natural habitats, (ii) as weeds in ruderal and cultivated habitats, derived from nearby natural populations, (iii) as wild types that have been brought into cultivation, without effective selection or domestication, and (iv) as weeds in ruderal and cultivated habitats, after dispersal from within cultivation.

In addition, domesticated forms of taro may become ruderal or wild after uncontrolled dispersal of seeds and vegetative parts, or after deliberate discard, or after being planted in the wild without cultivation. Many hard-to recognize categories of taro may also arise through uncontrolled breeding between wild and cultivated taros. To recognise wild-type taros, and to understand the history and ecology of wild taro populations, we must at least try to distinguish different categories, even if this is very difficult (cf. Table 1 in Matthews 1996). The essential starting point is simple observation and recording of taro in all its habitats.

Taxonomy

In this guide, I describe an apparently natural form or variety of taro (i.e., wild-type) and the wild habitats in which it has been found. This information is based on personal experience in Australia, New Guinea, Indonesia and the Ryukyu Islands of Japan (Matthews 1987, 1991, 1995; Matthews et al. 1992). The term 'variety' is used here in a

general and informal sense, to indicate phenotypic differentiation. Hay (1996; pers. comm.) urges that no formal infra-specific taxa be recognised presently in *Colocasia esculenta*, since reticulate relationships are likely to exist between wild-type(s) and cultivated forms of *C. esculenta*.

Previously (Matthews 1991, 1995), I identified *C. esculenta* var. *aquatilis* Hassk. (Hotta 1970) as a possible or likely wild-type. Henceforth, I will refer to the wild *aquatilis* as 'wild-type taro'. This identification is informal and has yet to gain wide recognition.

The practical problem of how to distinguish a wild-type from other categories of taro has been addressed in detail elsewhere (Matthews 1995). If other wild-types are found, then various options are possible for any formal revision of infraspecific taxonomy. Hay states that "we need to do the taxonomy of the wild taros from scratch throughout the entire natural range of the genus, and then see how cultivated forms are related to the wild entities that are recognised" (A. Hay, pers. comm.; paraphrase). This statement is consistent with the recommendations of Burt (1970).

Scope of the guide

From my own experience (mainly in low-altitude, tropical rainforest), the discovery of wild-type taro is greatly enhanced by focusing on habitats like those described below. Similar habitats exist in many areas that I have not explored. Other wild-types, and other species of *Colocasia*, may occupy different habitats in other vegetation zones (in tropical mountains or subtropical lowlands, for example).

The form presented here is designed for recording taro when time is limited during field exploration. With practice, the form can be completed in about 10 minutes. This form complements more elaborate protocols developed for taro in agricultural research collections (e.g., Whitney et al. 1939; Ghani 1984; Guarino and Jackson 1986; Hirai et al. 1989).

For botanical and ethnobotanical studies of taro, it is not always possible, practical, or necessary to collect whole plants for living collections or herbaria. When whole plants are not collected, it is especially important to record at least some phenotypic traits in the field. The form is based on experience gained during a survey in which leaf samples were collected from many sites, for DNA analysis. The form can be shortened, extended, or otherwise modified according to the particular purpose of the work. It can be used to record cultivated taro varieties, but is not intended as a substitute for the 1985 or later descriptor lists (Guarino and Jackson 1986).

Exploration for wild-type taro

In this section, I introduce the appearance, reproduction and habitats of wild-type taro (see comments on taxonomy, above). A general comparison with cultivated taros is presented in Table 1. The terms in bold face are illustrated in Figures 1 and 4.

Appearance

Wild-type taro is typically almost entirely an even, light green colour; the leaf blade has green veins and lamina; the petiole (leaf stem) is white at the base and green above,



Figure 1

without variegation. The junction of the petiole and the blade is red or purple in some leaves, in some populations. The side-shoots are long green stolons, with many nodes and often more than 1 m in length. The corm is generally small relative to the overall size of the plant, and has a white skin (outer epidermis). The corm core is composed of white storage parenchyma with pale yellow fibres. Loose and fibrous petiole remnants give the corm exterior a brown appearance; this fibrous tissue is easily scraped away to reveal the true skin colour. The true roots are white and coarse (often ea. 2 mm thick).

In wild locations, wild-type corms are usually watery and deficient in starch. Obviously escaped or transplanted cultivars are usually much more starchy. The amount of starch and degree of acidity may vary according to local conditions (water and nutrient supply) and according to season. Starch is often more abundant near the apex of the corm, just below the main shoot. Starch density can be assessed roughly by pressing the blade of a knife against the cross-section of a cut corm. A dense and opaque white liquid will appear if starch is plentiful.

The leaves and corms are very acrid, and the acidity persists after prolonged boiling or frying. Use extreme caution if acidity is to be tested by tasting: do not taste any raw tissue, and do not swallow the tissue or liquid, even after cooking. Acrid taro can irritate the mouth and throat severely and restrict breathing. A safe test can be carried out by rubbing freshly cut tissue against soft skin under the wrist. This produces an itchy effect that soon disappears.

Reproduction

Vegetative reproduction by stolons is obvious in all wild populations, and seed production is common, but almost no information is available regarding seed dispersal and germination. Male and female flowers occupy upper and lower portions of the same spadix. The spadix is covered by a spathe which is entirely green when young. The lower spathe remains green while the upper spathe becomes yellow or orange-yellow at

Table 1 Phenotypic variation in taro: summary for different plant parts in wild-type taro and cultivated varieties (from Matthews 1995)

Plant part	Components	Wild var. <i>aquatilis</i>	Variation among cultivated vars.	Comments
Leaf	blade and petiole	An even light green colour; red at junction of blade and petiole of some leaves in some populations; acidity strong	All parts of leaf: green or yellow-green and various red colours, in various graded and variegated patterns; acidity weak to strong	Variegations involve red and/or green pigments; complex colour combinations are common in cultivars
Inflorescence	spathe, spadix and flower parts	Components vary in size; the lower spathe and female flower parts lack red pigments	Components vary in size; the lower spathe and female flower parts may display red pigments	Complex colour combinations are common in cultivars
Corm	size and shape	Cylindrical, diameter usually = diameter of leaf base, size highly variable	Cylindrical to spherical, diameter usually > diameter of leaf base, size highly variable	Corm shape easily modified by environment, in variety-specific ways
	skin	White	White and various red colours; variegated or not	
	cortex	White	White and various red colours	
	core storage parenchyma	White; starch density low	White, various red, orange and mustard-yellow colours; variegated or not; starch density various, often very dense	Texture and flavour after cooking, and time to maturity highly variable among cultivars, rarely tested for wild var. <i>aquatilis</i>
	core fibres	White or pale yellow; coarse (thick) and high density	White, yellow and various red colours; various thickness and density	
	acridity (entire corm)	Strong	Weak to strong	
Roots	–	White	White and various red colours	
Side shoots	–	Long stolons, often >1 m in length (surface runners with shoots and roots at nodes)	In different cultivars: long to short stolons, direct shoots, elongate or round side-corms with starch	

maturity. The edges of the mature upper spathe separate to form a small aperture, and a sweet scent is released to attract pollinators. The stigma is sticky at this stage, before the anthers release pollen. The stigma and staminode are whitish or pale yellow. Pollen is released and adheres to the spadix as the spathe opens more fully. Eventually, the upper spathe and upper spadix wither and fall. If fertilization is complete, then the lower spadix develops into a swollen fruiting head with many fruit and several hundred seeds. The mature fruit are soft and green (or yellow-orange, according to Barrau 1959). Immature fruit are hard, shiny, and green. Mature taro seeds are hard, pale brown, and about 1.5 mm long with longitudinal corrugations that are visible to the naked eye. Immature seed are smaller, soft and have a smooth, pearly-white appearance.

Habitats

Wild-type taros grow next to permanent streams and waterfalls in wet tropical rainforest (Fig. 2) and next to permanent springs or seepages in monsoonal savannah. They do not grow in deep shade. Permanent populations of wild taro require stable substrates (rock or rarely eroded earth banks) and a permanent water supply. The long stolons follow wet crevices in rock, and the true roots enter these to form strong attachments. Corms and stolons are often washed downstream by floods. The presence of permanent or stable populations at higher locations (upstream) is often signaled by the presence of taro in lower, seasonally flooded positions, within the same stream or watershed. Vegetative growth is most vigorous in wet alluvial mud or silt with abundant sunshine. In such locations, stolons radiate out over wet surfaces, or through the substrates close to the surface.

In Australia, wild-type taro ranges from near sea level to almost 1000m asl, in the northern zones of tropical rainforest and tropical savannah. Stable and unstable habitats in Australia are illustrated in Figure 3. Ruderal habitats with apparently wild-type taro are usually wet ditches or banks, in open locations (with much sunlight) next to fields or roads (Australia, Indonesia, southern Japan).

Plant and site record form

The form has space for one plant, details about the site, and related data. The plant described should be typical for the variety and site. To record more examples of the same variety, or other varieties in the same site, use further pages (without repeating every detail in the form) or develop a new form with a more suitable layout.

Explanation of terms

Here I explain the underlined terms in the same sequence as they appear in the form. Self-explanatory or well-known terms are not covered. Many of the terms are illustrated in Fig. 4.

The record of date, site and variety (informal identification) can be incorporated into one alphanumeric sequence, the dsv number, e.g., 3.iv.96-1a indicates 'variety a' at the first site visited on 3 April 1996. If whole plants are collected for a living collection or herbarium, a more standard numbering system can be used.



Figure 2 Waterfall habitat of wild-type taro in Queensland rainforest. The heart-shaped leaves are visible at left in the splash zone near the bottom of the waterfall, and in a vertical crevice at the far right of the rock face.

The description of habitat should include indications of proximity to human settlement and activity (e.g., village, foot trail, gardening), local vegetation, geomorphological context (e.g. stream bank, waterfall), water supply (e.g., permanent, seasonal), aspect and exposure to light (e.g., open site on north side of stream, partial shade) and the kind of substrate (e.g., rock, alluvial mud, organic detritus, etc.).

The clump/shoot/leaf (csl) number identifies the first leaf to be measured on one shoot, within one clump. The first leaf measured is not necessarily the oldest or youngest emergent leaf. Within one site, there may be many taro clumps scattered over several or hundreds of metres. The spatial delimitation of sites should be discussed in later reports. For taro in wild locations, an arbitrary separation of 100+m or 400+m along the same stream or river can be used to assign clumps to different sites. For cultivated taros, the site can be defined as an individual field, garden, market or village. A clump is defined here as many plants side by side, with or without obvious vegetative connections. The term clump is convenient because there is often no secure basis for assigning separate shoots to a single clone (initial connections may rot).

A taro leaf consists of a petiole (leaf stalk) and blade. The distance pb, from the petiole base to the junction of petiole and blade, is easily measured by holding the end of a flexible metal tape measure against the base, and then pulling the tape case upwards - with both hands hooked around tape and petiole, to hold the tape and straighten the petiole.

To record the blade dimensions A-G in a consistent manner, use one hand to anchor

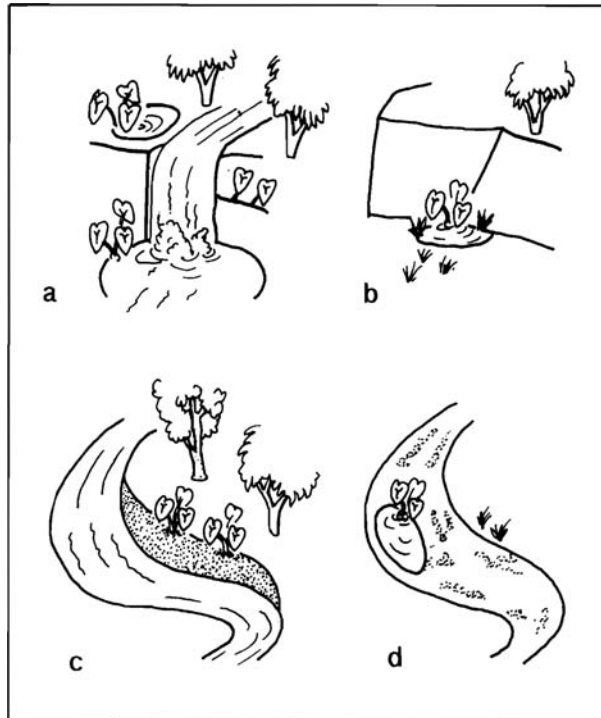


Figure 3 The habitats of wild-type taro: (a) stable habitats in tropical rainforest- waterfalls with permanently wet rock surfaces, in foothills and low tablelands; (b) stable habitats in tropical savannah permanent springs or seepages, at the foot of rocky escarpments; (c) unstable habitats in tropical rainforest- stream or riverbanks with soft substrate (plant detritus, gravel, mud, sand, silt); (d) unstable habitats in tropical savannah - lowland stream or riverbanks, on seasonal floodplains.

the tape measure on the upper blade surface. With large leaves, push one thumb through the blade from below, to anchor the tape above the point of petiole insertion. The anchoring hand can simultaneously rotate the leaf blade to assist measurement. It helps to have a second person, for writing as measurements are called out. The dimensions B and C are maximum distances to the margin or tip of each lobe, and do not always follow the main vein of each lobe.

The veins often curve or divide, so it is not easy to measure in a consistent manner. To measure G consistently, hold the rear of the leaf so that it is fully open without being artificially flattened.

In a previous study in New Zealand (Matthews 1984), the dimensions B, D, E and G were used in a canonical discriminant analysis of leaf shape. In a comparison of three different cultivars (distinguished before analysis), maximum discrimination was obtained by the contrast of large B and small D values with small B and large D values. The dimensions B, C and G were used to calculate the approximate angle between the rear

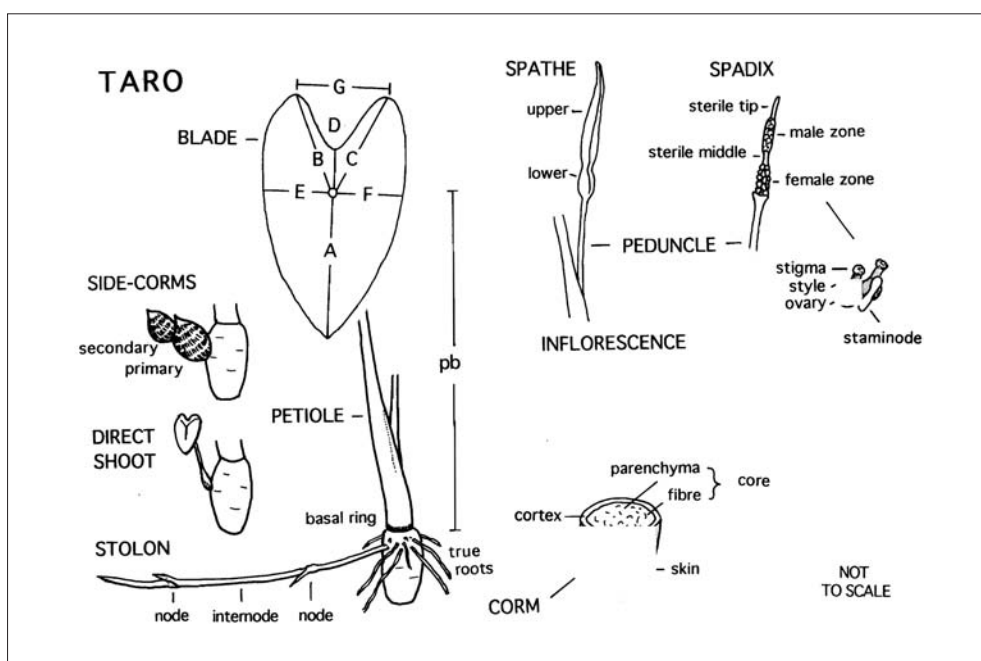


Figure 4 Schematic illustration of terms used to describe taro.

lobes in different cultivars: rear-lobe angle (degrees) = $2\sin^{-1}(G / B+C)$. This angle was also useful for distinguishing cultivars, despite difficulty in accurate measurement of G. Other derived characters were calculated as follows: symmetry = $(E \times B) / (F \times C)$, lobedness = $([B+C] / 2)1A$ and peltateness D/A .

It is difficult to make accurate or reliable verbal descriptions of colour. We can only expect to make approximate records. These are usually adequate for distinguishing a limited number of varieties in a limited geographical area. Common blade colours, in the main veins and lamina, are: red (R), pink (Pi), purple (Pu), dark purple or 'black' (Bl), green (G), and yellow (Y) or yellow green (Y-G). Similar colours can be seen in the petiole. The colour terms can be modified with adjectives such as dark, pale, light, dense. The main veins (central and lateral) are best viewed on the underside of the blade. Fine, tertiary veins contribute to the colour of the lamina (the flat tissue between the main veins).

Petiole colours often grade from one into another vertically, and the graded colours often form a background for attractive variegated colours. Again, the description can only be approximate. The vertical sequence of graded colours, from upper petiole to petiole base, can be indicated by placing a slash between each colour, e.g., G / Pu / W = green above grading into purple and white near the base. Variegated colours may be flecked, striped, or mottled, and the colours can be used as adjectives for each type of variegation, e.g., R fleck, Pu mottle, or W stripe.

Taro site record form		Page __ of __ pp.	
Location.....		Date/site/variety (dsv).....	
Habitat.....			
Local name of plant.....		Informant.....	
Sample: living/herbarium/other.....		Collector's specimen no.	
Photos: yes/no/photo file no.			
Vegetative parts Clump, shoot, & leaf (csi):/...../.....			
Leaf dimensions (cm): pb..... A..... B..... C..... D..... E..... G.....			
<u>Blade colour</u>		1. vein 2. lamina	
<u>Petiole colours</u>		3. graded+ variegated.....	
		4. basal ring colour.....	
<u>Roots</u>		5. thickness.....(mm) 6. colour.....	
<u>Corm part colours</u>		7. skin 8. cortex	
		9. core 10. fibres	
<u>Side-shoot type</u>		11. stolon/side-corm/direct shoot/other.....	
sketch:			
Inflorescence Absent/present: clump, shoot, & inflorescence (csi) number:/...../.....			
<u>Upper spathe colour:</u>		12. green/ yellow/orange/brown (withered/fallen)	
other:			
<u>Spathe zones (cm):</u>		13. upper..... 14. lower	
<u>Spadix zones (cm):</u>		15. female 16. sterile middle	
		17. male 18. sterile tip	
<u>Spadix colours:</u>		19. stigma 20. staminode	
<u>Fruit stage:</u>		21. unexpanded/ expanded & hard/expanded & soft	
<u>Seed stage:</u>		22. absent/immature/mature	
Notes: (Uses, ecology, fruit colour, etc)			

Figure 5

Petioles often display a complex combination of graded and variegated patterns involving green and purple colours (chlorophyll and anthocyanin pigments). A bronze appearance (Br) can be produced by the combination of graded green and purple colours. It is often a matter of subjective judgement whether or not to record two colours as one very fine variegation on a graded colour background, or as two graded colours, or as a single colour. The code G / Br can be used to indicate a predominantly green upper colour grading into bronze. If the purple pigments dominate in the lower part, then the description becomes G / Pu. If the purple pigments form a distinct variegation, then the

description becomes G / G+Pu fleck. If the upper petiole also has some purple, then the description can be Pu / G I/ G+Pu fleck.

The basal ring colour appears as a distinct ring at the very base of the petiole when an obvious anthocyanin pigment (Pu or R or Pi) lies next to a pale graded colour (e.g., W or G). If the main colour of the lower petiole is very dark, then the pale basal ring colour might not be visible, and a question mark should be noted.

Corm colours are often very simple (white in all parts), but anthocyanin pigments do appear in the skin, cortex and core. These pigments are usually similar to the those seen in the leaf, and can appear in variegated patterns. Mustard yellow (Mu) and orange (O) are colours that I have only seen in the core parenchyma; these are presumably carotenoid pigments (these have great potential as targets for breeding attractive cultivars; similar pigments have been important in other root crops). Fibre colours include white, pale yellow, and purple.

Side-shoots are highly variable in colour and morphology. Individual plants may display both direct shoots and stolons. Stolons are defined here as side-shoots in which at least the first internode has a narrow and constant diameter (the first internode lies between the parent corm and the first node). Without this it can be difficult to distinguish an elongate side-corm from a child corm mounted on a short stolon. An sidecorm can display a distinct (protruding) node on a swollen first internode.

The inflorescence also varies greatly in colour and morphology. The colours of peduncle and lower spathe are often similar to petiole colours on the same plant, so no space is given for recording these colours (the apparent correlation between petiole and inflorescence colour is intriguing; the latter is unlikely to have been the object of direct human selection).

The upper spathe colour varies according to developmental stage. It is yellow or orange-yellow when the female flowers are mature, which is when a sweet scent is emitted. The colour from green (G) at emergence from the petiole sheath, to yellow (Y), orange (O) and brown (B) at the onset of withering. Intermediate colours are also seen (Y-G, O-Y and B-O). Eventually, the upper spathe falls to the ground and a swollen fruiting head develops on the peduncle. Spathe and spadix zones vary in length according to variety and developmental stage. If the upper spathe colour is recorded, then the comparability of measurements from different plants and sites can be confirmed later. I usually measure the spathe and spadix when the upper spathe is yellow or orange-yellow.

Further notes can be added to record details of use, ecology, fruit and seed development, habitat, access, location, starch content, acidity, nearby human activity, insect associates and pollination, seed dispersal and germination, disease and other matters.

Acknowledgements

The author thanks Dr Alistair Hay (Royal Botanic Gardens, Sydney) for advice on the taxonomy of taro, and one anonymous reviewer for helpful comments.

Appendix 23. Two taros from Japan: *Ishikawa-wase* and *Tonoimo*

The following text is from an unpublished article, written in Kyoto, November 1993, and distributed as a flyer together with planting materials.

Two Japanese taro varieties were introduced to New Zealand for the first time in 1992. In this article I describe how the plants were introduced and their history in Japan. I also describe the new varieties so that they can be identified, and outline methods for cooking and cultivation. Words marked with an asterisk (*) are explained in a glossary at the end.



It will take time for us to learn how to grow the new varieties in New Zealand. Please try them — and good luck. Write to me if you have questions. I will answer if I can. After you have tried the new varieties, please tell me if they grew well or not. How did you grow them? Was the crop good? How did you cook them? Did you like the taste and texture of the corms? Please copy this article and pass it on.

The journey to New Zealand

On the 14th of April, 1992, I left Osaka with several tiny taro shoots inside small glass bottles. The shoots were a present from Masahiro Morishita at the Osaka Agriculture and Forestry Research Centre. Dr Morishita prepared the shoots and put them in bottles so that they could grow without any disease (see methods, Morishita 1988).

On the way back to Auckland, I stopped in Sydney. The quarantine office there looked after the shoots for three weeks, then brought them to the airport when I left. The shoots were allowed in at Auckland Airport because they were clean. I also had import papers that were sent to me before I left Japan. Many people already grow taro in New



Zealand, so I had to be careful not to bring sick plants into the country.

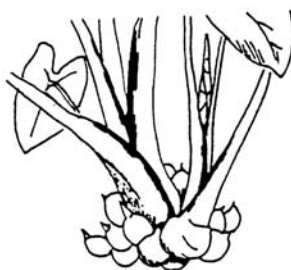
At the University of Auckland, Dr Lena Fraser looked after the shoots until they developed leaves and were strong enough to go into covered trays. The plants were ready to go outside just in time for the summer of 1992/93.

History and identification

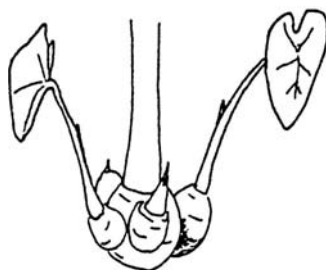
Ishikawa-wase and *Tonoimo* are both very popular in Japan. They are widely grown in home gardens and commercially (see Hirai et al. 1989).

Ishikawa-wase is a modern variety less than 200 years old. It probably originated as a spontaneous* new form in a farmer's field at Ishikawa, in Osaka. The likely parent is an old variety that is still grown. The change to a new variety may have involved a loss of purple colour in the leaf, a reduction in plant size, and an increase in the number of side-corms* produced.

Ishikawa-wase is usually less than one metre high at maturity, and produces many small round secondary and tertiary corms* in a cluster. The sheath has a distinctive brown-black margin.



Tonoimo is a very ancient variety. The name was recorded in 560 AD and means something like 'potato from China'. The plant has light-purple to green petioles*, and is 1–1.5m high at maturity (in good conditions). The primary and secondary corms are soft and tasty when cooked.



Cooking

In Japan, corms* are often boiled in water and flavoured afterwards with salt or sauce. They are also gently cooked in watery sauce until the sauce is absorbed. They are often added to soups. Never eat raw taro — it has poisons that protect the plant against animals.

Here is a simple method for cooking small corms, or pieces of larger corms:

- (1) boil in water for 5–10 minutes, then discard the water,
- (2) boil again for 5–10 minutes, in water or soup stock.

After cooking, the corms should be soft all the way through, without falling apart. Continue cooking if there is an itchy effect in the mouth or throat (there is no danger if you taste carefully, the effect goes away soon, drink milk as an antidote). Peel and cut large corms before cooking. Corms that are too small for peeling can be steamed in their skins (about 20 minutes). To peel a small corm after cooking, squeeze it gently with your fingers. The skin will crack, letting the inside part slip out in one piece.

The petioles of *Tonoimo* are also good for eating. The young petioles are best. Cut them into pieces and boil in water for 5 minutes, then use as a salad vegetable with dressing. Alternatively, cook them as part of a soup.

For Hawai'ian cooking methods, see Kokua (1982).

Distribution and cultivation

Wild and possibly natural taros are distributed all the way from northeastern India and southern China to northern Australia and Papua New Guinea. The first cultivation of taro was somewhere in this tropical region (Matthews 1991). For temperate countries with cold winters and short summers, selection by farmers was needed to develop varieties that could be grown easily. Taros in Japan, Korea, and central China have many starchy side-corms. The corms can be stored over winter, for eating or planting, and the starch helps the new leaf growth in spring.

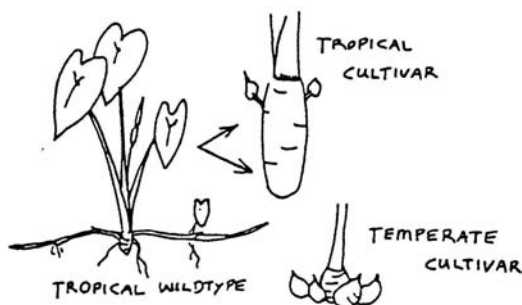
In tropical countries near the equator, the growth of taro is continuous because the climate is continuously warm and wet (Massal and Barrau 1956; Wang 1983). The corms can become very long and cylinder-shaped because of the continuous growth. Tropical taros often have one big central corm. The top can be harvested and then planted without any storage period. Big corms from Fiji, Tonga, and Samoa are sold in New Zealand.

Countries that are slightly north or south of the equator have wet and dry seasons instead of summer and winter. Taro can grow during the dry season if there is irrigation. Planting stocks can be kept growing in permanent streams or ponds, ready for the start of the wet season.

Taro also grows in warm-temperate countries around the Mediterranean Sea. It was a major vegetable in Cyprus up until the 1950s (Cristodoulou 1959), and was recorded as wild in streams in southern Spain in the 1920s. It is still grown in Egypt and Lebanon.

In cool-temperate parts of Japan, taro corms are stored during winter in a covered pit in the field, packed with straw, or in a cellar with good aeration. Primary and

secondary corms are eaten or planted according to the variety. Petioles are harvested during summer and can be dried for storage. Summer is usually quite hot in Japan, so taro patches are often planted in irrigated fields next to rice.



Cultivation in New Zealand

Taro is an ancient crop in New Zealand. It is most common in the northern half of the North Island (Matthews 1985; Part 2, this volume), but also grows in the Nelson district. Taro can survive outside during winter, but stops growing because of the cold temperatures and short days. Exposed shoots are damaged by frost. Shoots that were protected under old leaves or in the ground recover best, when summer comes .

Many trials will be needed to discover the best locations and methods for the Japanese varieties. Here are some suggestions to start with:

(1) For planting material, keep the sort of corms that you like best. Make them all one size if you want an even crop later. Don't take corms from plants that grew weakly or had strange colour patterns on the leaves — the plants may have some kind of disease. Virus and fungus diseases can spread with the corms.

(2) For an early start, plant corms before summer, after the days start becoming longer. In Auckland and further north, October may be a good month to begin planting. Put corms in a warm, sunny corner of the garden, or in a hothouse, until new shoots appear. When there is no danger of frost (if you have frost) the shoots can be moved to less sheltered positions.

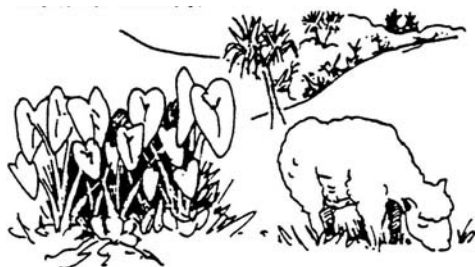
(3) Taros are very sensitive to soil structure, fertility, and water supply. They do well in loose, dark soil near streams and rivers. They often survive drought, but the outer leaves wilt and die quickly. A temporary drought will set plants back all summer. Less water is needed near the end of summer. Too much water encourages leaf growth, and reduces the amount of starch in the corms.

(4) Taros can also be grown without special effort. Plant shoots in a warm, sheltered place with soft soil, next to a ditch or stream that has water in the summer. A patch should develop without much further attention. Break up old clumps of corms, dig in the young side-corms, and pull down the old leaves that stick to the shoots. The old leaves can make it difficult for new leaves to come out. Use the old leaves as a mulch.

(5) Corms are best for eating at the end of summer or soon after (March to May),

depending on the location and variety (*Ishikawa-wase* is an early maturing variety, in Japan). Avoid old corms that are fibrous and watery. They take longer to cook and don't have much starch. A good corm is starchy all the way across, and from the base to the tip. The starch can be seen by pressing the surface in a cross-section. A white liquid should appear. Corm quality can also be judged by size and weight.

(6) There are many different ways to grow taro. The best way will depend on the location, variety, and the type of corm or leaf that you prefer. Try different varieties and cultivation methods, and make notes. If other people already grow taro in your area, ask them for advice!



Glossary

Corm: a storage organ that contains water and starch. Corms are swollen stems and are usually underground.

Petiole: the upright part of the taro leaf, connecting the corm with the leaf blade.

Primary, secondary and tertiary corms: primary - the central or mother corms; secondary - corms next to the mother corm; tertiary - corms growing from secondary or later corm.

Side-corms (cormels): secondary and tertiary corms.

Spontaneous new form: plant with a new shape or colour resulting from a change inside the plant, and not controlled by the farmer. No variety is completely stable. When taro is grown from shoots, the new plants are usually like the parent, but sometimes there are obvious differences. When new forms are noticed, and kept, they are often given a new name.

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