

Taxonomy and ethnobotany of *Colocasia esculenta* and *C. formosana* (Araceae): implications for the evolution, natural range, and domestication of taro

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ABSTRACT

A critical problem for the taxonomy of taro (*C. esculenta*), and for understanding the evolution and domestication of this species, is that there is no way to recognise, by simple visual inspection, a wild population of taro as part of a natural distribution. This is because people throughout Southeast Asia have long used wild taro as a

vegetable for human and animal consumption (as food and fodder). The example of *C. formosana* Hayata is introduced here because our observations so far indicate that this is a naturally-distributed wild species throughout its known range, despite its close phenotypic similarity to *C. esculenta*. To learn about the evolution, natural range, and domestication

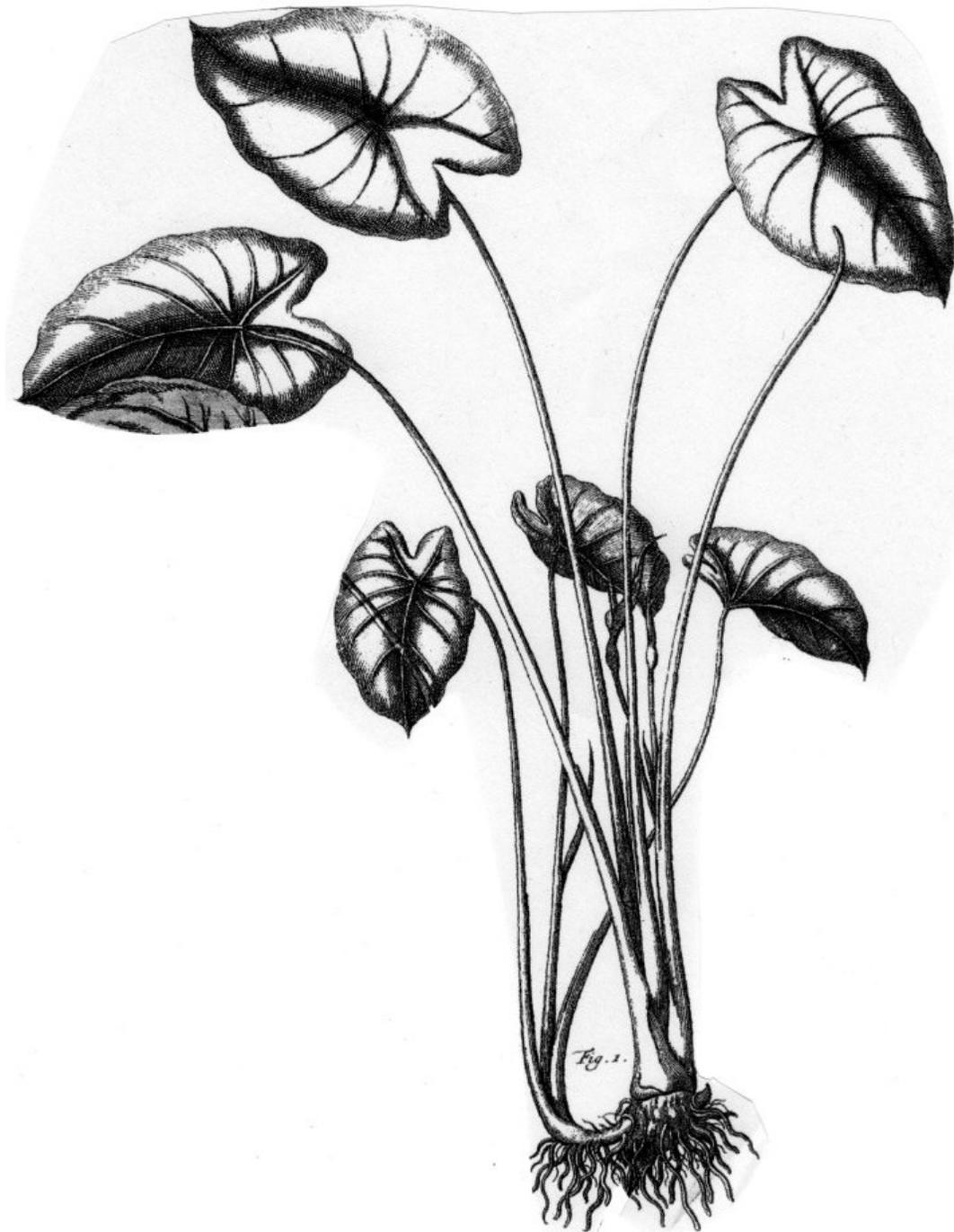


Figure 1 The “Water Kelady” (*Caladium aquatile*) illustrated by Rumphius 1741–50 (2011) in *The Ambonese Herbal*. Hasskarl (1848) referred to this work to establish the name *C. esculenta* Schott var. *aquatilis* (Rumph). The parent plant is flowering, and a new shoot has sprouted from the stolon at left.

of taro, closer study of *C. formosana* is recommended.

INTRODUCTION

The distribution, use, ecology, and genetics of wild forms of taro, *Colocasia esculenta* (L.) Schott, have been explored over many years in an attempt to discover the genetic and geographical origins of cultivated taro, a starchy root crop that is found in tropical to temperate regions of the world (Matthews, 2014). The current species name, *C. esculenta* (L.) Schott, is generally understood to refer to a single highly-polymorphic species, with several varieties, but historically there has been great uncertainty about definition of the varieties and their taxonomic status as botanical varieties or distinct species (Plucknett, 1983; Orchard 2006). The original descriptions for the species, and for two commonly recognised varieties, var. *esculenta* and var. *antiquorum* Hubbard & Rehder (1932) are all based on cultivated plants, while a third variety, var. *aquatilis* Hasskarl (1848) is based on an illustration and written description by Rumphius 1741–50 (2011) of an Indonesian wildtype or possibly naturalised (feral) wild taro (Hay, 1998). As a result, the polymorphism apparent in previous taxonomic descriptions reflects variation produced by human selection during domestication, as well as variation produced during natural evolution of the species. Rumphius gave two alternative Latin names for the same plant, based on where it could be seen growing: *Caladium vicorum* ('taro of the villages'), and *Caladium aquatile* ('aquatic taro'; also called

'water kelady' by Rumphius) (**Figure 1**). The ambiguity of its status as a wild plant seen growing in and around villages, and along rivers, is already apparent in the naming and description provided by Rumphius.

Formal descriptions of natural botanical varieties or sub-species should, in principle, be based on wildtypes present in naturally-distributed wild populations. According to the international codes of nomenclature for wild and cultivated plants (Spencer et al., 2007), a natural sub-species is 'generally understood as having defining characteristics that are usually geographically separated, although they may occupy different ecological niches', while a 'variety' is 'often understood as having characters that differ in a minor way' in plants that 'do not have a clearly defined geographical or ecological distribution'. A critical problem for the taxonomy of *C. esculenta*, and for understanding the evolution and domestication of this species, is that there is no way to recognise, by simple visual inspection, a wild population of taro as part of a natural distribution. We can assume neither that a particular patch of wild taro represents a natural variety or sub-species, nor that it is derived from cultivated plants. This is because people throughout Southeast Asia have long used wild taro as a vegetable for human and animal consumption (as food and fodder). The example of *C. formosana* Hayata 1919 is introduced here because our observations so far indicate that this is a naturally-distributed wild species throughout its

known range, despite its close phenotypic similarity to *C. esculenta*. For understanding the evolution and domestication of *C. esculenta*, there may be much to learn from closer study of *C. formosana*.

Previous theories of natural range and the origins of cultivated taro

Wild breeding populations of taro are distributed in tropical and subtropical regions from South Asia to East Asia, and through Southeast Asia to northern Australia and Papua New Guinea. In all these regions, there are many local uses for wild taro, which has served as a food source (corms, stolons, leaves, inflorescences, and - though rarely reported - fruit), medicinal plant, and as a fodder for domestic pig (Matthews et al., 2012; Masuno et al., 2012). Since wild forms of taro are useful plants, and are known from field interviews to be transplanted, it is not easy to distinguish naturally-distributed wild taro populations from populations that may arise directly or indirectly through human activities.

Following a survey of records of taro in botanical literature and European herbarium collections, and a survey of wild and apparently breeding populations of taro in northern Australia and Papua New Guinea (Matthews, 1987; 1990), maps were published showing the global distribution of taro in cultivation, the likely natural range of wild taro, and the distribution of two better-known wild species (*C. affinis*, *C. fallax*) (Matthews, 1991; 2006). Previously,

taro was most commonly known as a vegetatively propagated crop, and even today, it is still a surprise for many people to learn that wild breeding populations exist in many countries. In Queensland, Australia, inflorescences and fruit with seeds were seen in a large wild taro patch, in a region where taro is rarely cultivated. Many leaf samples were collected in transects through the patch, the leaves were frozen in liquid nitrogen, carried to a laboratory for DNA extraction, and the extracts were preserved in freezers from 1987 to the present day. Now it is known that taro DNA can be more easily sampled by simply drying the leaves in bags with silica gel. The 1987 samples were recently sent to the McDonald Institute for Archaeological Research in the United Kingdom for microsatellite DNA analysis, and our results provided the first genetic evidence of breeding in a wild taro population, while also indicating the predominance of one genetic clone in the taro patch studied (Hunt et al., 2013).

In Japan, and other regions of Northeast Asia, taro is cultivated at high latitudes that experience cold winters with snow. Under such conditions, farmers must give special care to ensure the survival of living plants from autumn until the next spring, despite the fact that the plants appear adapted to the cool and seasonal environment. The northern cultivars typically produce many side-corms that can be easily stored during winter, using storage methods that vary according to latitude and altitude (Matthews, 2002). The parent corms and child side-

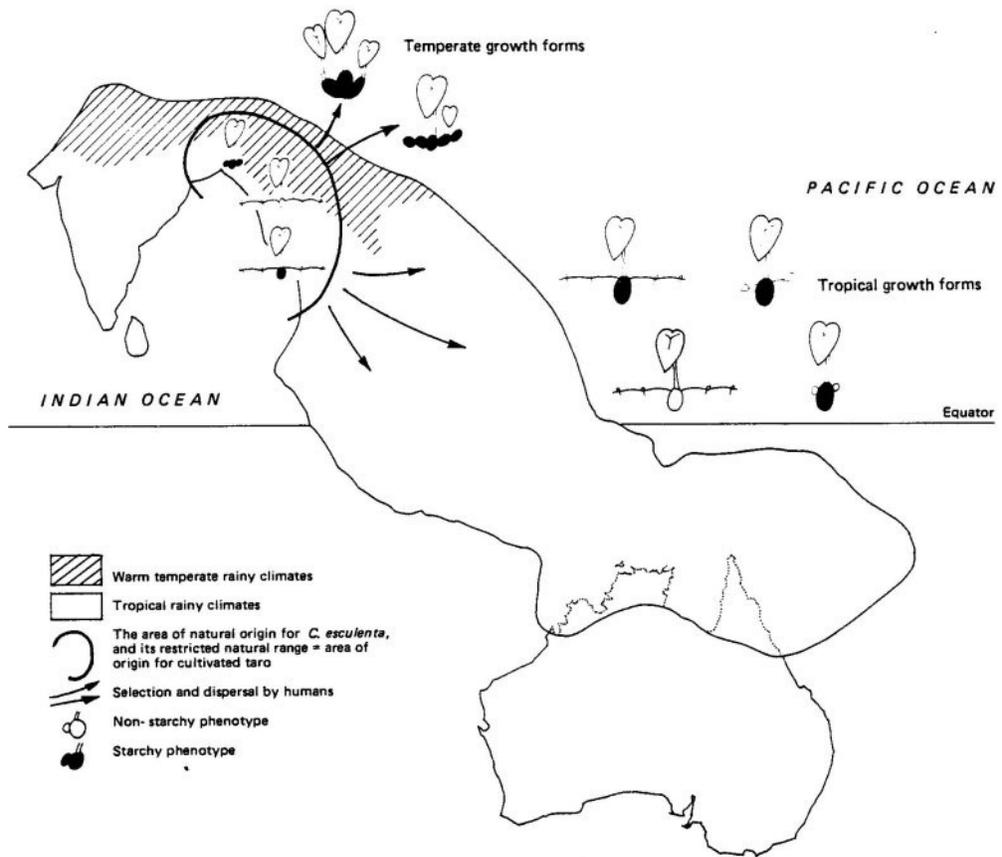


Figure 2. The possible *restricted natural range* of taro (*C. esculenta*), representing a single area of origin for cultivated taro in Southeast Asia. Diversity in the morphology of temperate and tropical cultivars is indicated outside the map boundary. In this scheme, wild populations in northern Australia and Papua New Guinea may have been derived from wild or cultivated forms introduced by people. The large area outlined, encompassing the region from India to northern Australia, is the maximum likely natural range (see **F3**) (from Matthews, 1990; 2014).

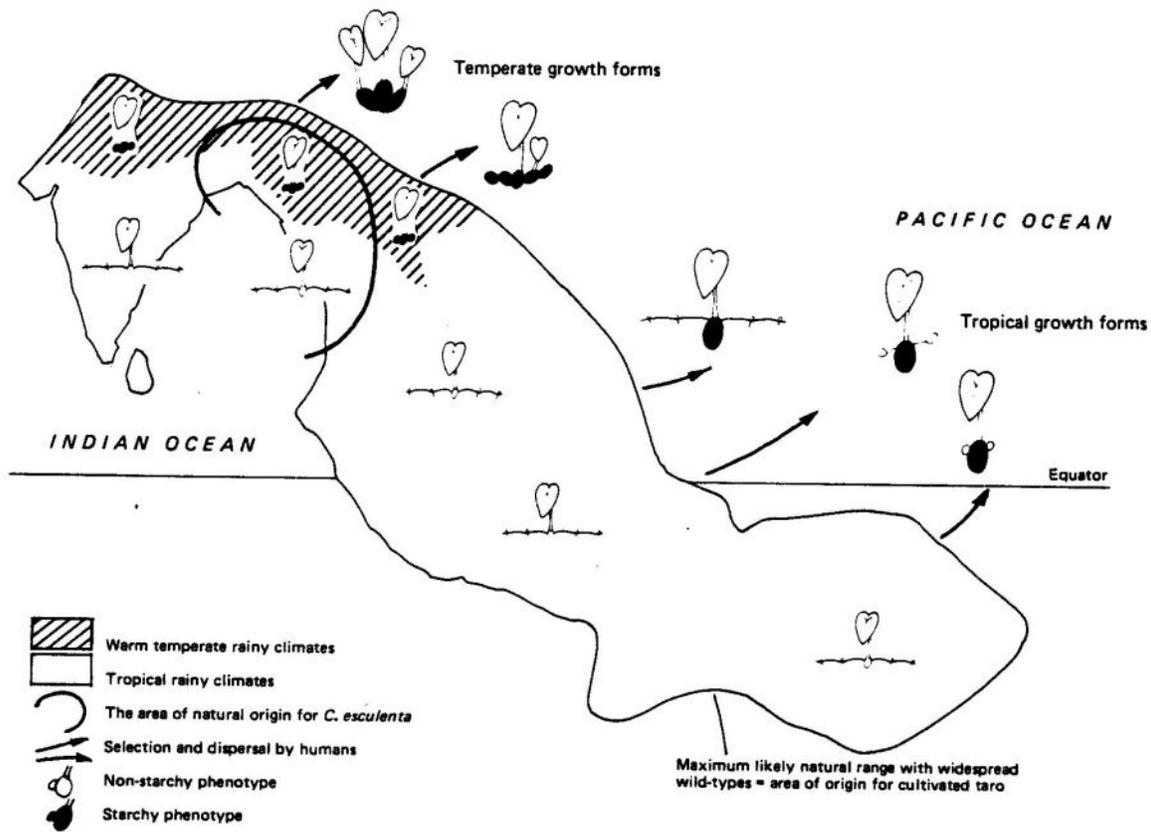


Figure 3. The *maximum likely natural range* for taro (*C. esculenta*), in Asia and the Pacific, and the possible multiple origins of cultivated forms throughout this range. In this scheme, wild taro in northern Australia and Papua New Guinea arrived first through natural dispersal. Diversity in the morphology of cultivated taro is indicated outside the map boundary. The possible area of natural origin for the species is unchanged from **F2** (from Matthews, 1990; 2014).

corms become dormant during winter, and carry many buds for regrowth in spring. Even with cold damage, and the death of some buds or shoots, the northern cultivars will sprout again in spring, and are easy to maintain.

The observations in tropical Australia and Papua New Guinea, and in temperate Japan, led to suggestion that there had been two main sources and directions for the domestication of taro (Matthews, 1990; 2014): (i) cool-adapted wild forms of taro the Himalayan mountains (somewhere in the region from northeast India to China) leading to the temperate adapted cultivars of taro (mainly triploids), and (ii) warm-adapted forms of taro in a tropical lowlands area (somewhere in the region from India to northern Australia and Papua New Guinea) leading to tropical cultivars.

Since little was known about the uses and dispersal of wild forms of taro, it was considered possible that the natural range of taro: (i) is restricted to a region of mainland Southeast Asia where mountain and lowland environments are present, within the vicinity of other wild *Colocasia* species known at that time (**Figure 2**), or (ii) extends throughout the region from India to Southeast Asia, northern Australia and Papua New Guinea (**Figure 3**).

In these figures, the maximum likely natural range of taro was identified according to the observations in northern Australia and Papua New Guinea, and

scattered records of wild taro in botanical literature and herbarium collections, for these and other regions (Matthews, 1991).

In the first scheme (**Figure 2**), the selection and dispersal of taro by humans began with starchy wildtypes that evolved and dispersed naturally within a range restricted to mainland Southeast Asia. This scheme followed the suggestion by Hotta (1983) (see also Hutterer, 1983), that root crops developed where species hibernated naturally in response to either seasonal dry periods or seasonal cold periods. 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 3**), selection and dispersal of taro by humans began with non-starchy wildtypes of wide natural occurrence, in tropical and warm temperate zones, respectively. In this case, it was suggested that starchiness increased in multiple areas of domestication, after breeding and selection in early farming systems, and specifically in early swidden systems or nursery plantings (Matthews, 1995). Such systems and plantings provide obvious opportunities for breeding among cultivar assemblages. Fallow gardens within the swidden cycle often include remnant plants that can be later reincorporated into active gardens, and during the fallow period, taro may breed, out of sight of the farmer.

In the many years since these two contrasting theories were proposed, new evidence has emerged concerning the economic uses of wild taro, the diversity

and distribution of wild species of *Colocasia*, the ecological requirements for wild breeding populations of taro, and genetic relationships among *Colocasia* species.

Below, we highlight some of the recent evidence, leaving genetic data aside, and recommend a focus on commensal wild populations and naturalisation in order to define natural range limits, and learn about the evolution and domestication of *C. esculenta*.

The uses of wild taro (*C. esculenta*)

Among cultivated taros, two main morphotypes are recognised: var. *esculenta*, with a large edible main corm and few cormels, and var. *antiquorum*, with a small or medium-sized main corm and a large number of small cormels (Plucknett, 1983). A wide range of intermediate forms is also known, as well as forms in which stolons appear to have become shortened and enlarged. In contrast to the great diversity of cultivated forms, the vegetative morphology of wild taros in warm regions of Southeast Asia to Australia and Papua New Guinea is relatively uniform (Ivancic & Lebot, 2000; Matthews, 1991;1997; Matthews & Naing, 2005; Matthews et al., 2012). Most wild taros do not display swelling of the corm relative to the leaf-base diameter at the corm apex (thus leading to elongate shapes in larger plants), and the corms are often fibrous and watery (less-starchy). However, such differences in corm dimensions and starchiness have not

been studied in detail under controlled conditions.

Although the corms of wild taros are generally considered by local people to be more acrid than those of cultivars, differences in acidity have also not been studied systematically. Acidity and starch production in wild taros are likely to vary according to both genotype and environmental conditions. Such variation may also be reflected in the different local uses of wild taros. Wild taro corms have been recorded historically as a useful but minor food, or as a famine food, in northern Australia (Scarlett, 1985; Matthews, 2014), Myanmar (Matthews & Naing, 2005), and southern Japan (Matthews et al., 1992), but not yet in Papua New Guinea (Matthews, 2014). In Australia and Papua New Guinea, the leaves and stolons of wild taro have not been reported as edible, but these parts are commonly eaten in China (Yang & Xu, 2000), Myanmar (Matthews & Naing, 2005), Philippines (Matthews et al., 2012), and Vietnam. Although the use of taro stolons is widespread, little has been reported regarding their variation, production, selection, utilisation, and nutritional value as vegetables.

In southern Japan (Matthews et al., 1992), Myanmar (Matthews & Naing, 2005), the Philippines (Matthews et al., 2012), and northern Vietnam (Matsuda & Nawata, 2002, Masuno et al., 2012), wild taro leaves are commonly cooked with other ingredients as a fodder for pigs. Use of wild

taro (**Figure 1**) as ‘a plain potherb for slaves and common people’, and as pig fodder, was reported in eastern Indonesia in the 18th century (Rumphius, 2011). Since pig husbandry is ancient in Southeast Asia, it is likely that the use of wild taro as a fodder for pigs is an ancient and widespread practice.

In the Philippines, wild taro was previously reported as absent or derived from cultivated populations. Wild taro today is common in warmer and wetter regions of the archipelago, and is used extensively and intensively as leaf vegetable for human consumption (Matthews et al., 2012). This may largely explain the general absence of flowering during our surveys, since cutting the plant tops prevents inflorescences from developing. A wild breeding population has been found in only one area, in northwestern Luzon, where wild plants are mainly used as a source of edible stolons. These can be harvested without obviously interfering with the flowering cycle (there may be non-obvious physiological consequences).

In Australia and Papua New Guinea, the use of wild taro leaves as a vegetable for human consumption has not been reported. This may explain why flowering, fruiting and seed production can be easily observed in wild taro patches (Matthews, 1990; 1995; Price et al., 2008; Hunt et al., 2013).

For human consumption especially, the risk of encountering strong acidity may be

the main factor that determines whether or not wild taros in a particular location or region are used and transplanted. Informants very often express concern about acidity when using wild taro corms, leaves, or stolons, and give various reasons for the occasional experience of acidity even after wild taro parts have been cooked (e.g., Matthews et al., 2012). Other less obvious anti-nutritional factors may also have contributed to whether or not wild taro plants were used in the past, and eventually domesticated (Matthews, 2010).

The widespread use of wild taro as a vegetable for human consumption, and as a fodder for pigs, was not known when the two models of domestication (above) were first proposed. The main difference between the two models is whether or not wild taros were widespread in Southeast Asia and the western Pacific before domestication, regardless of the manner of dispersal (natural, human transfer, or both). It is now clear that people can and do transplant both wild and domesticated taro into wild or disturbed habitats, for economic purposes, with or without interest in the use of corms for starch. At the same time, it is also clear that wild taros in tropical Asia and the Pacific can easily spread by natural means, through the production of sweet fruit that are attractive to birds and other animals.



Figure 4. *Colocasia formosana* Hayata from roadside at edge of forest, Mt Polis, Ifugao, Philippines, in 2011. The leaves display typical rounded shape with a relatively shallow sinus. Note fruiting heads at left, and young stolon emerging at right. The overall green colour and indeterminate stolon growth of *C. formosana* are also common in wild populations of *C. esculenta* (L.) Schott.



Figure 5. Fruit of wild *Colocasia formosana* Hayata, in Taiwan, 2008. The fruit of this species can be used as a bait to catch birds in simple spring-noose snares (Yuasa, 2000).

Hutterer (1983) and Matthews (1996) emphasized that the common distinction between ‘wild’ and ‘cultivated’ is not the same as the distinction between a wildtype (natural genotype) and domesticate (genetically modified through human selection). Cultivars can be wildtypes, and domesticates can enter wild habitats and become naturalised. Pollen and seed may disperse more-or-less freely between the different habitats. Wildtype plants can also be introduced to geographical areas outside

their natural range, and then become naturalised. Nevertheless, in regions where wild breeding populations are present, an individual plant found in a wild breeding population can be regarded as a possible wildtype, and the likelihood of this being true increases when local people regard the plant as wild, or naturally-occurring, or as inedible, and if they give the wild plant a different name from the cultivated forms they are familiar with.

In our fieldwork in Southeast Asia and the Pacific, we have focused on collecting possible wildtype taros, and recording information on their uses, in order to:

- (i) Compare genetic variation in different wild taro populations,
- (ii) Compare genetic variation in wild and cultivated taros,
- (iii) Look for correlations between usage and genotype among wild taros.

Wild populations that are not used, or are little-used, and that are genetically distinct from cultivated taros, are more likely to be naturally-occurring wild populations. Combining ethnobotanical and genetic data to characterise different wild taro populations, may eventually make it possible to distinguish naturally-distributed populations and those derived from cultivars through introduction and naturalisation.

Wild (non-cultivated) species of *Colocasia* are more diverse and widespread than previously thought

The genus *Colocasia* Schott is now believed to contain at least twelve and perhaps many more distinct species, all of which are found in humid to semi-aquatic habitats in Southeast Asia to southern China. The closely related genera *Ariopsis*, *Stuednera* and *Remusatia* include mainly shade-loving species (in the understorey of tropical

forests), and are native to the Himalayan region, though their distributions may range further (Bown, 2000). The following list of wild *Colocasia* species (not complete) is illustrative for the present discussion. More than half the known species of *Colocasia* have been described within the last 20 years.

1. *C. affinis* Schott 1859, wild in Southeast Asia (including Northeast India), lower altitudes.
2. *C. boyceana* Gogoi and Borah 2013, wild in Arunachal Pradesh, Northeast India, at altitudes of 1200–1600 m.
3. *C. debangensis* Gogoi and Borah 2013, wild in Arunachal Pradesh, Northeast India, at altitudes of 1800–2200 m.
4. *C. fallax*, Schott 1859, wild in Northeast India.
5. *C. formosana* Hayata 1919, abundant and widespread in Taiwan, where it forms a morphologically homogeneous wild population and is not known as a domesticate; it is morphologically distinct, but minimally so, from wild *C. esculenta*.
6. *C. gaoligongensis* H. Li & C.-L. Long 1999, wild in high mountains, Yunnan, at 3,700 m asl.
7. *C. libengiae* Long & Liu 2001 wild in mountains, northern Vietnam to Yunnan, China. The known range of this species was

recently extended to Arunachal Pradesh in Northeast India (Gogoi & Borah, 2013).

8. *C. menglaensis* Yin, Li & Xu 2004, wild in mountains, northern Vietnam to Yunnan, China.

9. *C. oresbia* Hay 1996, wild on Mt Kinabalu, Borneo, Malaysia (also in Bangladesh, according to Ara & Hassan, 2005).

10. *C. yunnanensis* Long & Cai 2006, wild in mountains, Yunnan, China.

The evolutionary origin of *C. esculenta* was previously considered to be somewhere in the vicinity of Northeast India, because that is where the greatest diversity of other wild *Colocasia* species was known (**Figures 2 and 3**). Now we can see that wild *Colocasia* species are spread over a huge region, from India to southern China and Malaysia. Within the expanded region of known diversity in *Colocasia* species, further unknown species are likely to be located in steep and inaccessible mountain valleys at altitudes between 400 and 4,000 metres.

The diversification of *Colocasia* species in Himalaya may reflect gradual uplift of the mountain ranges, and repeated cycles of warmer and cooler climate, over many millions of years. As mountain populations became increasingly isolated, they may have given rise to new species. Somewhere in this mountain zone of speciation, *C. esculenta* may have evolved as a low-elevation plant adapted to warm, sunny, and constantly wet

environments, in contrast to the cooler, shadier, drier, and more elevated environments occupied by most of its wild relatives. Although the full diversity of species in *Colocasia* is not yet known, recent fieldwork and genetic analyses (Ahmed, 2013; Ahmed et al., 2013) suggests that three wild species may be of special significance for the evolution and domestication of *C. esculenta*, namely: *C. libengiae* and *C. yunnanensis* (both sister species?) and *C. formosana* (a recently evolved species derived from taro?). In this paper, we give particular attention to *C. formosana*.

Wild breeding populations require warm and wet conditions, and insect pollinators

In experimental living taro collections that are not subject to harvesting, flowering is common. In temperate regions such as central Japan and northern New Zealand, floral development is quickly terminated by the arrival of cold winter conditions (Matthews, 1985; 1995; 2014), and require glasshouse heating and hand pollination for breeding experiments in central Japan (cf. Yoshino, 2002). The present authors have observed wild breeding populations, with fruit and seed production, in Papua New Guinea, northern Australia, Myanmar, northern Vietnam, northern Philippines, and northern India. In Papua New Guinea, seedlings are common on wet ground around the fruiting parent plants. When collected from ripe fruit, and planted immediately, taro seeds germinate after

about two weeks at room temperature, when sown on wet soil in a covered container.

It is likely that the most sensitive stage in the life cycle is when young seedlings are first establishing roots, as the seedlings quickly die or become stunted if they experience drought under laboratory conditions. In tropical to subtropical regions, warm temperatures and continuously damp or wet ground conditions appear to be ideal for wild breeding populations. Young plants may grow slowly in shaded micro-environments near the parent plants, or wherever deposited by animal agents, but once established, it is likely that they can quickly take advantage of any available sunlight (for example, when a canopy gap exists or is created by vegetation disturbance). In laboratory experiments with taro seeds and seedlings, the rate of growth and size of taro seedlings can easily be controlled by restricting or increasing available nutrients and light (unpublished notes, Field Sciences Laboratory, National Museum of Ethnology). The young seedlings require only water and little light, but are very tolerant of low or high nutrient conditions, and low or high light conditions. When placed in fertile soil, in larger pots, with more light, the plants quickly increase in size. In wild taro patches, the flowering individuals are usually larger plants growing in sunny positions with deep soil.

Another important requirement for successful breeding by taro is the presence

of more-or-less specialised insect pollinators. When *Colocasiomyia* spp. (Drosophilidae) were first observed on taro in Papua New Guinea and Southeast Asia, it was believed that they were very host-specific (Carson & Okada, 1980; Matthews, 2014). This may be true where wild plant populations and the insects have co-existed in a stable environment for long periods. However, when the host plants are moved into new environments by transplantation, or when the host plants naturally disperse and mix with other aroid taxa in disturbed habitats, ecological relationships between host plants and insect pollinators may change rapidly. It is now known that *Colocasiomyia* spp. are able to move between *Alocasia* spp. as host plants (Miyake & Yafuso, 2005), and here (Table 1) we report the presence on *Colocasia* spp. of *Colocasiomyia steudnerae*, which was first observed on *Steudnera* (Takenaka et al., 2006). When pollen are moved between different genera, sterile hybrid offspring may be produced like those described by Yoshino (2002). When pollen is carried between previously-isolated but closely-related species in the same genus, hybridisation might occur easily. If hybrid individuals become isolated from their parent species, and form a new breeding population, then a new species of hybrid origin may emerge. The causes and consequences of hybridisation are thus closely linked to pollen flow, plant dispersal, and any changes in environment that affect the relative fitness of parent and hybrid populations.

In northern Vietnam, while travelling by road from the lowlands to the mountain area of Sapa, and in the hills around Sapa, we collected *Colocasiomyia* samples at various altitudes from the inflorescences of *C. esculenta*, *C. libengiae*, *C. menglaensis*, and *C. yunnanensis*. The associations found (Table 1) suggest that the diversity of pollinators is higher in the mountain zone where multiple wild species of *Colocasia* are present. However, the collecting region is a region where there has been both ancient and modern intrusion of farmers and settlements into the mountains, creating new opportunities for the expansion of

existing wild *Colocasia* species, and also introducing *C. esculenta* as a cultigen into close proximity with those species. The full range of possible genetic interactions between the different host taxa, and between the different pollinator taxa, is unknown. With the insect pollinators present and able to follow the floral scents of different host plants, there may be a double-synergy of diversification in host plant populations and diversification in the pollinators. This is a clearly a region where much can be learned about the ecology and genetic potentials of wild and cultivated *Colocasia* species.

Table 1. Multiple species of *Colocasiomyia* (Drosophilidae) associated with *Colocasia* species in northern Vietnam. Samples collected by Matthews and Nguyen Van Dzu in 2012. Summary data based on initial identifications provided by M. J. Toda, Hokkaido University Museum.

Host <i>Colocasia</i> species	<i>Colocasiomyia</i> species identified			
	<i>xenalocasiae</i>	<i>alocasiae</i>	<i>steudnerae</i>	other spp.
<i>C. esculenta</i>	+	+	+	+
<i>C. yunnanensis</i>	+	-	+	+
<i>C. libengiae</i>	+	-	+	+
<i>C. sp.</i> Mau Son	-	-	-	sp. 2 aff. <i>iskandari</i>
<i>C. gigantea</i>	+	+	-	+

Is *Colocasia formosana* Hayata a distinct species?

Japanese botanists who observed, collected, and first described *Colocasia formosana* Hayata (1919) in Taiwan in the early 20th century came from a country

with no wild breeding population of taro, and a cultivar assemblage dominated by cool-adapted, triploid forms of *C. esculenta*. Most cultivars known to them in central or northern Japan would have displayed leaves with a dark-green upper surface and pale

lower surface, together with starchy mother corms and many side-corms (i.e., the morphotype of *C. esculenta* var. *antiquorum*). From the cultivar assemblages of southern Japan and Taiwan, they may also have been familiar with plants producing large starchy corms and few side-corms (i.e. the morphotype of *C. esculenta* var. *esculenta*) (Plucknett, 1983). For them, wild *C. formosana* must have appeared very different from all the known cultivated forms of taro.

In recent years, the diversity of Japanese taro cultivars has been quite thoroughly described in morphological and genetic terms (Hirai et al., 1989; Matsuda 2002), and a wild form of taro, *C. esculenta* var. *aquatilis*, has been reported in Okinawa, southern Japan, where it is not known to breed (Hotta, 1970; Matthews et al., 1992). This plant is likely to have been introduced as an edible wild vegetable or as a fodder plant from Southeast Asia. Phenotypically similar wild taros are common throughout Southeast Asia, New Guinea, and across northern Australia, but are not uniform in their chloroplast DNA sequences (Ahmed, 2013). These wild taros often form breeding populations in wet open habitats, and are most abundant in the vicinity of human settlements. In terms of overall plant colour (green), and vegetative morphology (relatively small corms and long stolons), they are generally more similar to *C. formosana* in appearance than tropical and temperate cultivars, but their acidity and morphology do vary, across Asia and the Pacific, and remain to be compared systematically. In morphological terms, *C.*

formosana is not clearly distinct from *C. esculenta*. In our experience, all traits described in the original species description (Hayata, 1919) lie within the range of variation of *C. esculenta*.

Recently, we have discovered a small number of apparently isolated populations of *C. formosana* in wet mountainous regions of Luzon, in the northern and central Philippines (**Figure 4**). In both Taiwan and the Philippines, *C. formosana* is known to be very acrid, and is generally not regarded as an edible wild vegetable, though methods for preparing the plant to make it edible are known. Detailed studies of the ethnobotany of this species are needed, but already it appears to be a much less useful plant than wild *C. esculenta*, which is so widely used as a vegetable and fodder plant in Southeast Asia (see above).

The populations of *C. formosana* found until now, in Taiwan and the Philippines, appear homogeneous in colour and general morphology, and are readily recognised in the field because of a very rounded leaf blade with shallow sinus. All inflorescences seen on plants in the Philippines and Taiwan have a long sterile appendage, like that found on the original type specimen from northern Taiwan, and the proportions of different parts of the spadix are quite uniform. Fruit colour in wild *C. esculenta* varies from bright orange/red in Myanmar (Matthews & Naing, 2005) to a yellowish-brown colour in Papua New Guinea (Price et al., 2008). Fruit colour in *C. esculenta* generally (including wild and cultivated

forms) ranges from green to orange and purple (Ivancic & Lebot, 2000). Thus, the bright orange/red fruit colour of *C. formosana* (**Figure 5**) is not a distinguishing trait, though it is consistent within the species.

The northern distribution of *C. formosana* in island Southeast Asia hints at a natural presence of the species in southern China, and dispersal eastwards from there, following or before a split from *C. esculenta*, or within *C. esculenta*. The northern distribution also lends support to the model of wide natural range (for *C. esculenta*) as suggested in **Figure 3**, assuming that *C. formosana* is derived from *C. esculenta*. A genetic bottleneck, in *C. esculenta* or *C. formosana*, could have arisen during long distance dispersal from a mainland source region, and/or increasing isolation in Taiwan as a result of rising sea level and changing climate (during the late Pleistocene, for example). Genetic comparisons of the known populations in Taiwan and the Philippines might provide evidence for movement of *C. formosana* from west to east, from Taiwan to the Philippines.

Naturalisation and crop domestication

It is difficult to investigate the natural history, domestication, and dispersal of taro, when so many uncertainties remain in the basic description of closely-related species and their distributions. Where did *C. esculenta* originate as a natural biological species, and how many species are really

encompassed by the current taxonomic concept of *C. esculenta*? Most wild species of *Colocasia*, and especially those that have been described only recently, are known from relatively few locations. Future exploration to map these species in wet monsoonal regions of Asia might also reveal further new species of *Colocasia*, and these might include new candidates for involvement in the domestication of taro. The optimal search space for *Colocasia* as a genus is gaining definition, and predictive mapping methods can be developed and used for the genus as a whole, and for particular known species.

On morphological grounds it is difficult to support *C. formosana* as a species separate from *C. esculenta*, but since *C. esculenta* is itself poorly circumscribed, we cannot reject *C. formosana* without further study. In the future, when wild populations of *C. esculenta* are better known, it may be necessary and possible to split *C. esculenta* into multiple species, or subspecies, based on wildtypes of defined natural range rather than basing the taxonomy on a mix of wild and cultivated forms with poorly known distributions. This brings us back to the problem of how to recognise wildtypes in a species, or species-complex, when the plants can easily naturalise and perhaps hybridise. A broad answer to this conundrum is that we must integrate ethnobotanical, ecological, and genetic approaches to the study of the genus and its species.

In particular, our priorities should be: (i) Systematic comparison of different wild

populations of taro (*C. esculenta*), within the full range of wild species of *Colocasia*. Of special interest are the genetic relationships between wild and cultivated taro in lowland to mountain habitats in Asia and the western Pacific. (ii) Genetic testing for introgression and hybridisation among wild *Colocasia* species, including *C. esculenta*, during the evolution and domestication of taro. (iii) Ecological study of seed production, dispersal and germination, and also the distribution, host range, habitat requirements, and diversity of insect pollinators, in order to understand how seed dispersal and pollination may limit or promote hybridisation and speciation in the genus *Colocasia*. (iv) Ethnobotanical study of the uses and management of wild taro (*C. esculenta*) and other wild *Colocasia* species that may have been involved in the evolution and domestication of taro. This, along with the ecological approaches, will help us to understand the role of commensal and naturalised populations in the historical development and domestication of the crop.

It may be no exaggeration to say that for 99% of living crop species, there has been little or no consideration of how human activities might have extended the geographical range of wild populations, or of naturalisation as a long-term historical process. Ignoring the problem of how to recognise natural range is convenient for biological studies, because it simplifies the interpretation of genetic variation in wild populations, and comparison between wild forms and cultivars. For understanding crop

history, however, this problem must be faced directly. Plant taxonomists have nevertheless helped circumscribe the problem through their studies on aroid taxonomy and the genus *Colocasia* in particular. Knowing more about the wild species of *Colocasia* makes it easier to recognise the outer limits of diversity within *C. esculenta*, which in turn makes it possible to define geographical limits for the species as a whole.

To recognise and locate the genetic and geographical origins of cultivated taro, we must continue looking for ways to recognise and map natural wild populations in this species. This work is difficult because it requires the combined efforts of many researchers, in collaboration with diverse local communities, using diverse local languages. The work is also difficult because natural wild populations can also have economic significance, which makes it impossible to exclude the possibility of a human role in their biological history.

In Southeast Asia, the uses of wild taro as food and fodder are significant contemporary economic activities. They are likely to have started long before domestication of the crop. They also link the history of taro to the history and domestication of pig, itself an important component of economic history in Southeast Asia. Range extension to new habitats and new regions, and naturalisation in new habitats (e.g. ruderal habitats in cleared land) and new regions (outside the true natural range), could be central to

domestication in taro, in terms of the process, without necessarily being central in terms of the geography.

Naturalisation is a process that can create new breeding populations that are to some degree isolated from natural wild populations with undesirable traits. In crosses between selected (favoured) cultivars and wild taros in any given area, the offspring are likely to be poor and not favoured, unless people are in the habit of using the particular wild parent plants involved, or existing cultivars are not much different from the wild plants (as might be the case during an early period of domestication), or the wild plants belong to a population derived from cultivated forms, through naturalisation.

In the last case, the naturalised population might consist of a mixture of clones derived from cultivation, and their sexual offspring, thus retaining the favoured traits of parent cultivars, or producing new combinations that are potentially superior to those of the parents. In modern breeding trials in Papua New Guinea, using wild taro as a source of disease resistance was very difficult because the genetic basis of resistance was not easily separated from undesirable qualities introduced from wild parents that may have been natural wildtypes. Even with deliberate backcrossing, assessment, and selection, it was difficult to produce acceptable new cultivars using unscreened wild parent plants (Ivancic & Lebot, 2000).

Naturalisation as a central focus for research

In many areas of Southeast Asia, including the Philippines and Vietnam, naturalised populations derived from cultivated taro are likely to be the main sources of wild taro as a food and fodder plant. Since ancient times, such populations might have been important for the generation of new cultivars, including cultivars resistant to pests and diseases. Commensal wild populations present in and around human settlements may or may not be naturalised, or deliberately spread. This uncertainty is not a reason to ignore them as 'invasive weeds', or too difficult to study, or of secondary historical importance. Over thousands of years, naturalised populations may have had central and continuing roles in the primary and secondary domestication of taro. Defining the natural range of taro (**Figures 2 and 3**) is a necessary challenge for evolutionary study of the species, and has helped bring the process of naturalisation into focus. To develop more realistic models for the evolution and domestication of taro, and many crops, it may help to make naturalisation a central focus of research. Further taxonomic and ethnobotanical studies will also help in the development of models that embrace commensal wild populations and naturalisation. The phenomenon of natural wild populations becoming 'denaturalised' or commensalized, as they spread by natural dispersal into human environments, is also of interest. This can be seen in Taiwan, where *C. formosana* has been found (in just

one location, to date) in an agricultural lowland near forested mountains.

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