A POSSIBLE TROPICAL WILDTYPE TARO: *COLOCASIA ESCULENTA* VAR. *AQUATILIS*

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INTRODUCTION

Interpretations of natural range and variation are prerequisites for understanding the selection, propagation and dispersal of taro by humans. In addressing the question of geographical origin, many writers have not been explicit about whether they mean the origins of taro as a natural species or the origins of varieties of cultivated taro. In this paper I develop a theoretical framework for investigating the origins of taro as a species, and the origins of cultivated varieties of this species.

If *Colocasia esculenta* (L.) Schott (taro) originated somewhere as a natural species and the geographical range of this species was not extended by humans before its cultivation, then cultivated varieties must have originated within the natural geographical range. Observation of other *Colocasia* species and of wild taro suggests the possibility of a natural range extending from northeast India to Australia and New Guinea. If taro was this widespread before its cultivation, then the varieties cultivated today may have diverse and independent origins. A common tropical wildtype, known in the botanical literature as *C. esculenta* var. *aquatilis*, is identified here as a possible basis for the selection and domestication of taro over a wide geographical range.

Early authors who tried to identify naturally occurring wild taro could not distinguish between plants ultimately derived from cultivated introductions and those of natural occurrence, as reviewed by Spier (1951). This continuing problem has been restated by Hotta (1983) and Matthews (1987) and 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). Debate about taro and the origins of Asian and Pacific agriculture has been reviewed by Spriggs (1982) and is summarised by Matthews and Terauchi (1990). Here I present previously inaccessible but important botanical evidence which suggests that the geographical origin of taro is somewhere within northeast India or Southeast Asia. I then summarise field observations of wild taro in Australia and Papua New Guinea and discuss the possibility that they are extreme

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southern and eastern examples of a widespread tropical wildtype, *C. esculenta* var. *aquatilis*. The term "wildtype"' is used here to signify a natural variety which may or may not be located within its natural geographical range.

HISTORICAL RECORDS AND RECENT FIELD OBSERVATIONS

There are few published accounts of *Colocasia* species other than *C. esculenta*, the most comprehensive being that by Engler and Krause (1920). The distributions shown in Figure 1 are based on herbarium specimens seen by the present author and on living specimens received from various sources (Appendix). Sighted were ten provenanced specimens of *C. fallax*, 12 of *C. affinis* and 28 of *C. gigantea*. Hotta (1970; 1983) has recorded *C. indica* (a synonym for *C. gigantea*) in Borneo, and this is noted in Figure 1. Three species not recorded in Figure 1 are known from only one specimen each. These are *C. gracilis* Engl. from Sumatra, *C. mannii* Hook. f. from upper Assam and *C. virosa* Kunth from Bengal. The distribution shown for taro is based on herbarium specimens seen but too numerous to be listed.

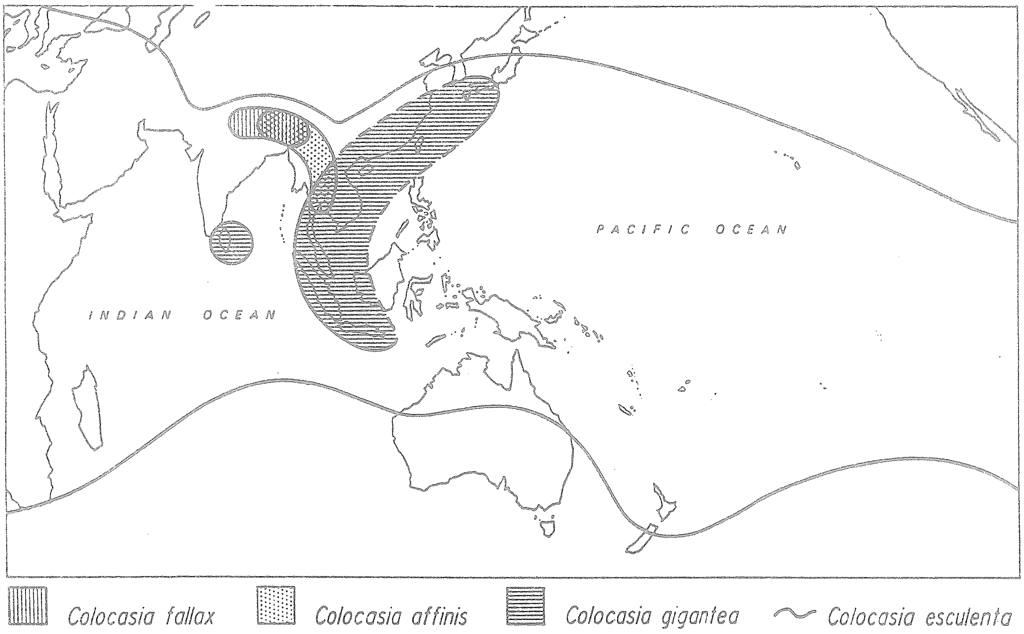

FIGURE 1: THE DISTRIBUTIONS OF *COLOCASIA* SPECIES
C. esculenta ranges from Africa to South America. Dotted lines indicate where the boundaries for *C. gigantea* are most uncertain.

Records of wild taro in Australia in the period from 1770 to 1989 are restricted to the climatic zone of tropical summer rainfall (Figure 2). A detailed account of published records, herbarium specimens and recent field observations is given by Matthews (1990:52, 382-395) and is summarised in Table 1.

FIGURE 2: THE GENERAL DISTRIBUTION OF WILD TARO IN AUSTRALIA, BASED ON RECORDS FROM 1770 TO 1989

The dark areas are where taro have been recorded, all within the climatic zone of tropical summer rainfall.

	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

TABLE 1: RECORDS OF WILD TARO IN AUSTRALIA

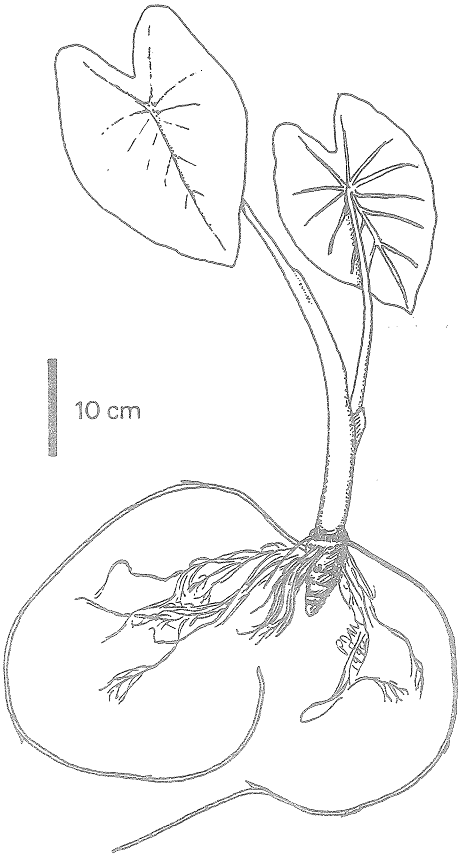

FIGURE 3: WILD TARO FROM TROPICAL RAINFOREST, RUSSELL RIVER, NORTHEAST QUEENSLAND, AUSTRALIA.

Typical phenotype for Australian wild taro. Leaf: the blade has green veins and lamina; the petiole is white at the base and green above, without variegation. Lateral shoots: long stolons with many nodes. Corm: small with low starch density; the skin, cortex parenchyma and core parenchyma are white; the core fibres are yellow. Roots: white and coarse (1-2 mm thick).

Wild taro are widely distributed but generally rare, in very localised patches associated with permanent water, in the Kimberley region of Western Australia (K. Kineally and S. Forbes, pers. comm. 1985), Arnhem Land in the Northern Territory (R. Jones, pers. comm. 1989) and Kakadu National Park in the Northern Territory (Russell-Smith 1984). The wet-tropical rainforest zone of northeast Queensland was surveyed by the present author in 1987 because early ethnographic and botanical records and the reports of Queensland correspondents indicated that wild taro is relatively common there, and because access was easier than in the more northern areas. Wild taro were found next to streams and rivers in forests near the Queensland coast and in coastal lowland areas now dominated by sugar-cane plantations. The earliest record of taro in Australia is that of Joseph Banks (1770), who collected taro near the Endeavour River in northeast Queensland in 1770. Taro were recorded near this river at some time between 1858 and 1866 by A. Thozet (Melbourne Herbarium sheet 1560160), in 1882 by Persietz (Melbourne Herbarium sheet 1560159), at the end of the last century by Roth (1901) and in 1987 by the present author.

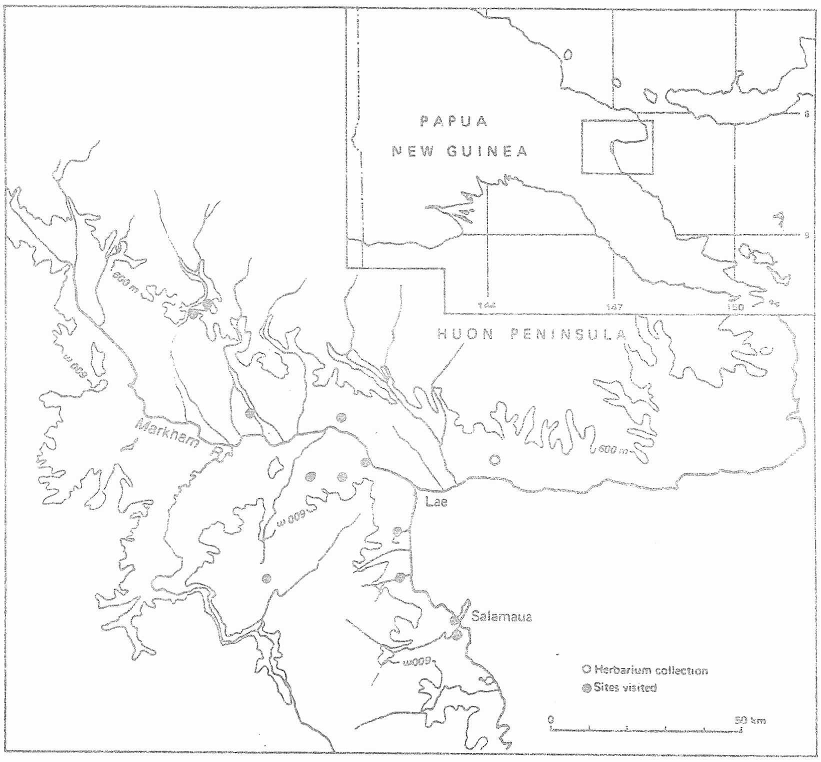

FIGURE 4: LOCATIONS OF STOLONIFEROUS WILD TARO NEAR LAE, PAPUA NEW GUINEA. The search, in July and August 1985, was largely limited to areas below 600 m. One record from a well-described herbarium specimen is included (Jermy # 4460, 1964/65, British Museum).

Wild taro in Australia are almost all entirely green and all produce long stolons (vegetative side-shoots) and small central corms with very little starch (Figure 3). Flowers, fruit and seed were found in Queensland, suggesting the possibility of natural long-distance dispersal by fruit and seed, if suitable animal vectors are also present. In a brief visit to Papua New Guinea in 1985, wild taro with flowers, fruit and seed were also found, alongside streams or rivers, in and adjacent to lowland rainforests near Lae (Figure 4). The phenotypes of these plants were generally very similar to those in Australia.

THE ORIGINS OF TARO AS A NATURAL SPECIES

Because all the other species of *Colocasia* are confined to northeast India and Southeast Asia, *C. esculenta* probably originated in this region, as suggested by previous authors for the same reason (Engler and Krause 1920; Hotta 1983). If phylogenetic relationships between *Colocasia* species can be determined, then it may be possible to locate the origin of *C. esculenta* more closely, within or close to the geographical range of its nearest relative.

Engler and Krause (1920) placed *C. gigantea* Hook. f. (synonymous with *C. indica* [Lour.] Hassk.) in a Section Caulescentes, separate from the 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 species in morphological aspects of the leaf, inflorescence, fruit and seed (Engler and Krause 1920; personal observations). Initial tests suggest that the mitochondrial DNA of *C. gigantea* is more closely related to that of another genus, *Alocasia*, than it is to the mitochondrial DNA in other species of *Colocasia* (Matthews 1990:141). The other species of *Colocasia* are thus more likely to include the nearest relative of *C. esculenta*. The restricted mainland ranges of *C. fallax* and *C. affinis* (Figure 1) are probably the natural ranges of these species since both are little utilised. Hen (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 in shrublands.. *C. affinis* var. *jenningsii* is a rare ornamental cultivar outside mainland Asia (personal observation) and human dispersal of this variety as an ornamental could have extended the range of *C. affinis* within mainland Asia. No other records for the utilisation of these species have been found. It seems unlikely that they were cultivated in the past, so taro is unlikely to have evolved from them within agricultural contexts. It is more probable that taro first evolved as a natural species, from wild progenitors not yet identified, somewhere within the region of northeast India and mainland Southeast Asia.

THE MAXIMUM POSSIBLE NATURAL RANGE OF TARO

If *C. esculenta* originated as a natural species within the region of northeast India and mainland Southeast Asia, as suggested above, then this area must also include all or part of the natural range of taro. Natural occurrences beyond this region remain unproven. Ferdinand von Mueller (1865-66) described taro as apparently indigenous in the warmer parts of eastern Australia, while Cheeseman (1900) reported taro as truly native in India and Malaya and probably also in some Pacific Islands. More recently, Yen (1982) and Coates *et al.* (1988) have 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. No published statements are known regarding possible natural occurrences of taro west or northeast of the likely area of species origin.

The present range of cultivated taro in Asia follows two major geographical and climatic axes. On an approximately west to east axis, from India to New Guinea, tropical rainy climates are found. These include perhumid climates close to the equator and monsoon climates with progressively longer seasonal dry periods further north and south (Whitmore 1984:55). On a north to south axis, from southern India and Southeast Asia to northern India and northern China, climates range from the tropical rainy types just described to temperate and cold-temperate rainy climates at the northern limit of cultivated taro. On these axes, four major barriers define the maximum possible natural range of taro: (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) states that the diversity of the eastern tropical 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 dubiously endemic species of *Raphidophora*. The natural range of taro may extend as far as New Guinea or slightly further east. The Malesian floristic region, in which many aroids occur, extends eastward as far as the Bismarck Archipelago, a floristic 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, large ocean gaps are almost certainly major barriers for the natural dispersal of taro.

An absence of botanical records in northern China (*cf.* Hen 1979) and arguments for the origins of Japanese cultivars in southern China (Takayanagi 1986) suggest a possible northernmost limit within the temperate region of China. Populations of what might be naturally occurring wildtypes have not been described for temperate northern latitudes, but might exist. Wild taro are not known in the arid or temperate zones of Australia (Figure 2), despite extensive botanical exploration of the continent during the last two centuries. The possible southernmost natural limit of taro in northern Australia appears relatively well defined.

C. ESCULENTA VAR. *AQUATILIS*

Stoloniferous wild taro identified as *C. esculenta* var. *aquatilis* (Hassk.) Kitamura (Hotta 1970) are known in Bengal, Malaysia, the Ryukyu Islands and Java (Engler and Krause 1920; Hotta 1970). It is suggested here that the wild stoloniferous taro of Australia and Papua New Guinea also belong to this variety. An adequate and formal identification is not yet possible because the existing descriptions of var. *aquatilis* are based on floral and vegetative characters that are likely to be polymorphic within the variety. It is hoped that the variety can be better defined and recognised in the future by DNA analysis and by statistical comparisons of phenotypic variation among living specimens. Haines (1924) presented a type description for *C. antiquorum* Schott var. *stolonifera* Haines, which he regarded as similar to the Javan var. *aquatilis* Hassk. The variety of Haines was found wild and flowering along rivers near Ranchi and Palaman, Bihar Province, eastern India, in 1918 (Kew Herbarium sheets 4381, 4382) and is described as having green leaves and numerous long stolons, up to 3 m in length. This description is consistent with the wild phenotype common in Australia and Papua New Guinea, as is the description of var. *aquatilis* Hassk. by Engler and Krause (1920) and Hotta (1970). Mitra (1958) reported that *C. antiquorum* var. *nymphaeifolium* (Vent.) Engl. is wild throughout eastern India and Bengal. Hotta (1970) placed this variety within the taxon *C. esculenta* var. *aquatilis* [Hassk.] Kitamura. The type locality of var. *aquatilis* Hassk. is Java (Engler and Krause 1920), but the general distribution of this variety within Indonesia is not known. Backer and Bakhuizen van den Brink (1968) describe the species *C. esculenta* as wild at low altitudes in Java (0-250 m), on watersides, in sudds, swamps and waste places and in *Barringtonia* formations.

Two traits shared by *C. fallax, C. affinis, C. gigantea* and wild taro in Australia and Papua New Guinea are the stoloniferous growth habit and the production of very little starch in the central corm, as observed in living specimens by the author. If these traits belonged to a single common ancestor, then they might have been present in the earliest forms of taro, within the region of northeast India and mainland Southeast Asia, a region which is generally monsoonal. In northern Australia, where a strongly seasonal, dry/wet monsoon climate prevails, the stolons of wild taro can extend horizontally for at least 2 m, with nodes from which new shoots and stolons are produced. When water is scarce, stolons grow in the direction from which water originates. As water-seeking generative organs, stolons appear to be an alternative to starch storage and dormancy for survival in monsoonal regions. Sauer (1952:40, cited by Hawkes 1989:482) states that underground starchy reserves help plants to survive dry seasons and regenerate quickly when rains return. Stoloniferous wild taro grow in permanently wet sites in monsoonal and non-monsoonal areas, so the stoloniferous habit did not necessarily evolve in response to monsoonal dry periods. If this habit was the original state of taro, then its retention may have lessened any advantage in starch storage as a response to seasonal aridity. Perhumid rainforest at one extreme of habitat and monsoonal savanna at another could both have accommodated the dispersal of *C. esculenta* var. *aquatilis* by natural means, or by humans before cultivation of the species.

THE ORIGINS OF CULTIVATED TARO VARIETIES

If taro spread naturally throughout what is now mainland and island Southeast Asia and into Australia, New Guinea and the periodic landbridge connection between them (the Sahul shelf), then wild populations probably differentiated in partial isolation from each other in diverse ecological circumstances. Different ribosomal DNA variants have been found in different wild populations of what are identified here as *C. esculenta* var. *aquatilis* in Australia and Papua New Guinea (Matthews 1990; Matthews and Terauchi 1990). This apparently widespread wildtype differentiated at as yet unknown times and locations within or west of the Australia/New Guinea landmass. Early natural differentiation of var. *aquatilis* could have created diverse circumstances for later selection by humans in tropical areas from northeast India to Australia/New Guinea.

Was starch production the only prerequisite for the initial selection and cultivation of taro? Other traits such as medicinal properties or the edibility of shoots and leaves might have enhanced the usefulness of taro, or might have been sufficiently useful in their own right. If plants were initially cultivated as leaf vegetables, then poor yields of starch 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 for multiple purposes, including the provision of starch, before cultivation began.

The examples of var. *aquatilis* found in Australia and Papua New Guinea produce very little starch (author's observations). Although this may have been typical for the variety throughout its range before agriculture, alternative uses could have encouraged cultivation, creating opportunities for the selection of more starchy varieties. 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. Specimens seen by the author in the field and in herbaria and reports by many others (Shaw 1975; Strauss *et al.* 1979; Sunell and Arditti 1983; Nyman and Arditti 1985) support the view that wild taro flower and produce viable seed abundantly throughout tropical parts of Asia and the Pacific. Occasional harvests and replanting of feral and other wild varieties, or protection of useful wild varieties when old and new garden areas were cleared, could have brought many sexual progeny, with new genotypes, into assemblages of vegetatively maintained cultivars. In this way, swiddening systems probably provided ideal circumstances for breeding and selection.

Hotta (1983) has suggested that there are several separate genealogies of cultivated taro originating among diverse starchy wildtypes within a natural range limited to mainland Southeast Asia. This followed from his general suggestion that root crops in eastern Asia developed where species stored starch and became dormant in natural response to either seasonal dry periods or seasonal cold periods. Here I suggest that var. *aquatilis* is a never-dormant tropical wildtype which was possibly cultivated and domesticated over a wide geographical range, within and beyond eastern Asia. Early selection and dispersal was not necessarily associated with agriculture and early utilisation for products other than starch could have been important.

CONCLUSION

The actual significance of human dispersal of wild taro before cultivation of the species is completely unknown. Under the hypothesis of domestication over a wide geographical range, a restricted natural range remains as strong a theoretical possibility as a wide natural range.

If genotypic characters now under investigation are diagnostic for the tropical wildtype var. *aquatilis*, then it is predicted that the same characters will help to distinguish tropical and temperate genealogies of cultivated taro.

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APPENDIX: RECORDS OF *COLOCASIA* SPECIES

Herbarium specimens in European herbaria, 1984 and 1985, not including those with insecure determinations (*cf.* Matthews 1990:408-410). For each specimen the following are noted: location and (collection date), *collector's name* and field number (or herbarium number, with herbarium prefix) and (herbarium) locations. The locations of type specimens are noted. 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. Three living field collections of *C. gigantea* are also noted. For a list of all herbaria searched, see Matthews 1990:382.

C. fallax Schott (Engler and Krause 1920)

Darjeeling, India (1875), *Clarke* 29237 (K), det. anon; Pir Pauce, Khasia Hills, India (1850), *Hooker and Thompson* (K, Type), det. Schott; Himalayas, India (pre-1893), ex hortus Herrenhausen, *Engler* 240 (K,B,LG), det. Engler; Dehra Dun, North West Province, India (1898), *Gamble* 26994 (K), det. anon; Dehra Dun (1898), *Gamble* 27041 (K), det. anon; Lidi Khola, Nepal (1954), *Stainton, Sykes & Williams* 6801 (BM), det. Nicolson; Shidam Khola, Walna, Nepal (1954), *Stainton, Sykes & Williams* 5165 (BM), det. Nicolson; Ranchi/Palaman, India (1918), *Haines* 4440 (K), det. Haines; Garhwal Dun, W. Himalaya, India (1902), *Jacquel* 27017 (K), det. anon; Singbhum, India (1900), *Haines* 318 (K), det. Haines.

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; Silhet, India (pre-1920), *Wallich* 8952A (LG), det. Engler & Krause (1920); Manipur, India (1945/46), *Bullock* (K), c.f. *affinis*, det. Sivadasan (almost certainly var. *jenningsii*, my note); Pasay City, Philippines, recorded as an ornamental (1955), *Steiner* 683A (L), *C. esculentum*, det. anon. (leaf colour pattern indicates *C. affinis* var. *jenningsii*, my note); Doi Suthep, Chiengmai, 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.

Java (pre-1844), *collector*?, 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. (the fruit and blade indicate *C. gigantea*, my note); 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), details missing; Hong Kong (1905), *Cavalerie* 2506 (E), det. Nicolson; Buitenzorg, 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; vic. Chumphon, 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. anon; 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. (inflorescence immature but blade typical for this species, my note); Sumatra (year?), *Jacquinot* 472 (P), det. Nicolson. Live collections: Colombo, Sri Lanka (1986), *Amarasinghe* (ANU live coll. T321), det. P. Matthews; Rayong, Chantaburi, Chonburi, Thailand (1986), *Yen* 6 (ANU live coll. T357), det. P. Matthews; Hoshidate, Iriomote Is., Okinawa, Japan (1982), *Kobayashi & Sakamoto* 82.1.18.1.1 (ANU live coll. T311), det. T. Kawahara.

C. gracilis Engl.

Padang Province, Sumatra, Indonesia (pre-1920), *Beccari* (B, Type), det. Krause.

C. mannii Hook. f.

Upper Assam at Makum, India (pre-1920), *Mann* (K, Type), det. Engler & Krause (1920).

C. virosa Kunth

Bengal, India (pre-1920), *Roxburgh*, original illustration for Roxburghiana, Aroideae (K), det. Engler & Krause (1920).