

## Taro planthoppers (*Tarophagus* spp.) in Australia and the origins of taro (*Colocasia esculenta*) in Oceania

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### Abstract

Taro planthoppers (*Tarophagus* spp.) may be associated exclusively or primarily with taro (*Colocasia esculenta*), and the geographical distribution of *T. proserpina* provides circumstantial evidence that taro is native to the Sahul continental region (as well as being native to Sunda). *T. colocasiae* (Matsumura) (Asche and Wilson 1989a,b) is reported here for the first time in Australia, and the genus *Tarophagus* is reported for the first time on the wildtype form of taro (*C. esculenta*). Three species of taro plant hopper are present in Asia and the Pacific. *T. proserpina* has a relatively narrow distribution extending from eastern New Guinea to Polynesia (Remote Oceania). This distribution adds support to the suggestion that Polynesian taros are derived from a Melanesian taro gene pool. It is tentatively suggested that different *Tarophagus* species evolved in association with different taro gene pools, before the domestication of taro in multiple regions within Asia and the Pacific. Plant viruses associated with taro and *Tarophagus* are also discussed.

Insect associations with cultivated plants are important for many reasons, most notably because insects are often major pests and can also transmit various diseases. The economic impacts of insects on crops in the past are rarely known or knowable, although archaeologists have found storage pests (weevils) among archaeological remains of cereal crops (Vartavan 1990). Spriggs (1982) noted the possibility of archaeological preservation of insects associated specifically with taro, giving *Papuana* spp. (taro beetles) and *Tarophagus proserpina* (taro planthopper) as examples. Both genera are well known as agricultural pests on cultivated taro (Gagné 1982). Another way to approach agricultural history is to investigate the biogeography of living insects associated with living plants. This is the approach that I will introduce here with respect to taro, *Colocasia esculenta* (L.) Schott.

In July 1985, near Lae, in Papua New Guinea, I observed an insect pollinator, *Drosophilella pistilicola*, on wildtype taro in an area where these drosophilid flies had only recently been discovered and described by Carson and Okada (1980, 1982). Although sparse, the existing literature on *Drosophilella* strongly suggested that wild taro populations in Melanesia could be native

(indigenous) to the region (Matthews 1990, 1995). Subsequently, in Australia, I found large numbers of another insect, *Tarophagus* (literally, 'taro-eating'), on wild and apparently wildtype taros in the coastal region near Cairns, Northeast Queensland, in wet tropical rainforest. In this paper, I introduce the genus *Tarophagus* and its species in Asia and the Pacific, report my own findings of *Tarophagus* in Australia, and then interpret the distributions of *Tarophagus* species in relation to the origins of taro in Oceania. I also discuss plant viruses associated with taro (the host) and *Tarophagus* (the vector), and recent studies suggesting that there are multiple taro gene pools in Asia and the Pacific.

In this approach to the history of taro I am crossing disciplinary boundaries, just as I did during 1985 to 1990 as a student of Doug Yen, in the Department of Prehistory headed by Jack Golson, at the Australian National University (ANU). Both scholars encouraged me in this dangerous activity, while making clear the perils of treating any one discipline in too shallow a fashion. Another teacher at ANU was David Shaw, an entomologist who encouraged a healthy respect for the difficulties of biological observation and interpretation. Although digging deeply as an archaeologist continues to elude me as an occupation, I am still digging, as best I can, in other fields that can contribute to our understanding of the past.

### Tarophagus ecology, taxonomy, and geographical range

The taro planthopper genus, *Tarophagus*, has three recognised species, and these are considered important insect pests on taro. The entire life history of a taro planthopper occurs on taro leaves, above ground. Taro planthoppers feed on sap and heavy infestations can cause plants to wilt and become stunted. Feeding and egg-laying punctures cause sap exudation which forms red encrustations on the plant. The planthoppers are also vectors of taro bobone virus (a rhabdovirus), and this is of concern for taro growers because the resulting disease can stunt or kill plants. *Tarophagus* species are widely distributed from East Asia (including Taiwan and the Ryukyu Islands of southern Japan), through Southeast Asia to Australia (Northern Territory and Queensland), Papua New Guinea, New Caledonia, and many Pacific island countries (Gagné 1982, Zettler *et al.* 1989, Asche and Wilson

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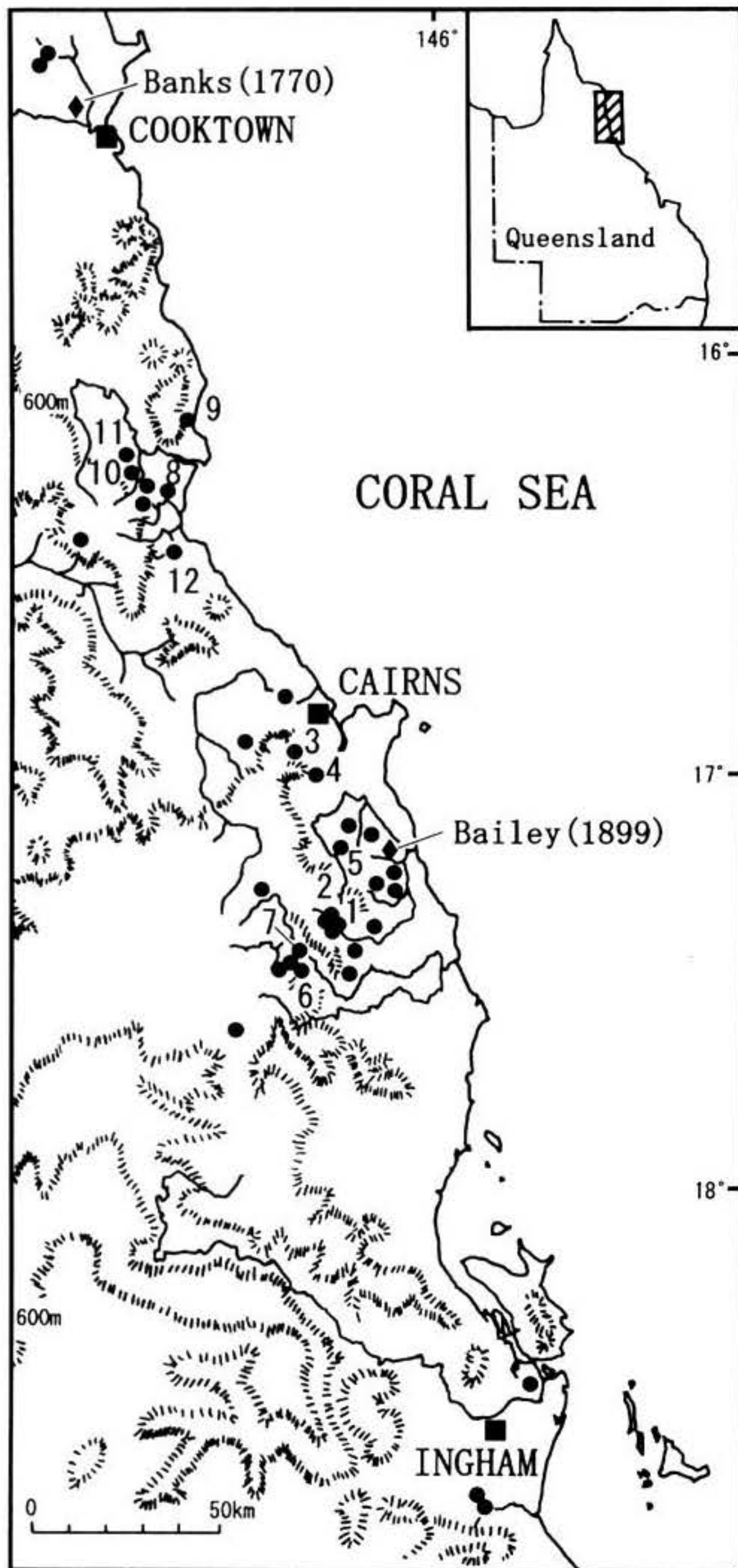


Figure 1. Map of wildtype taro sites in Queensland, 1987 and 1992. *Tarophagus* was found at the sites numbered 1–12 (see Table 1 for details). Illustration adapted from Matthews (1990). Early historical reports of taro (diamonds) are labeled with name of observer and date.

1989a, b). Eggs are laid in the bases of petioles and the midribs of leaves. Young nymphs are creamy white, and later stages develop predominantly black with white markings. From egg to adult takes about 18 days. These details may vary according to species, and have not been studied with reference to the taxonomic descriptions provided by Asche and Wilson (1989a, b).

*Tarophagus* belongs to the family Delphacidae, a large insect group in which most species feed on grasses. Many of them are pests on crops such as rice, sugarcane, wheat, rye, corn, and forage crops (Kisimoto 1994, Fletcher and Larivière 2001). Delphacid planthoppers are characterised by two wing forms (short and long) that appear either in both sexes or in one of the two. The long-winged forms can fly long distances. For example, in 1967, huge numbers of migrating rice planthoppers were discovered on a weather observation boat floating on the Pacific Ocean, at least 500 km distant from the Japanese mainland (Ichikawa 1994). The possibility of transoceanic migration by the taro planthopper has not been investigated. If taro is the only host for *Tarophagus* (or in regions where no other hosts are present), effective transoceanic migration by flight would require (or might be made possible) by the prior establishment of natural or introduced populations of taro, at every destination.

The known range of the genus *Tarophagus* is tropical to subtropical, with no reports from northern Japan or from New Zealand, at the northern and southern limits of cultivated taro in Asia and the Pacific. In Japan and New Zealand, cold temperatures and the winter loss of leaves by temperate-adapted forms of taro might prevent overwintering and survival of *Tarophagus*. The genus has not been reported in Sub-Saharan Africa (see Smithsonian 2001), although taro is an ancient and widespread crop in Africa.

Asche and Wilson (1989a) noted that taro planthoppers were identified in most previous reports as *T. proserpina* (Kirkaldy). After looking at specimens from throughout Southeast Asia and Oceania, these authors recognised three morphologically distinct species, *T. colocasiae*, *T. persephone*, and *T. proserpina*. The known distributions of these species (see later) overlap and together span most of the possible natural range of taro (Matthews 1991, 1995, 1997), as well as extending into Remote Oceania where taro is an entirely introduced crop. So far, *Tarophagus* has only been reported on taro (*Colocasia esculenta*). Other species of *Colocasia* are mostly non-domesticated, wild species located in mainland and island Southeast Asia. The presence or absence of *Tarophagus* on these close relatives of taro has not been investigated. In the following sections, *T. colocasiae* is reported for the first time in Australia, and the association of *Tarophagus* with wildtype taro, in natural habitats, is also reported for the first time. Although *T. persephone* (Kirkaldy) was reported in Northern Territory and Queensland by previous authors, the host and habitats were not described.

#### Field work and collection methods

Field surveys in Queensland, Australia, were carried out during the dry season, in September 1987 (Matthews 1990) and again in August 1992 (Matthews 1992). The primary aim of these surveys was to locate and describe wild taros and their habitats (Figs. 1 and 2). Taro plan-



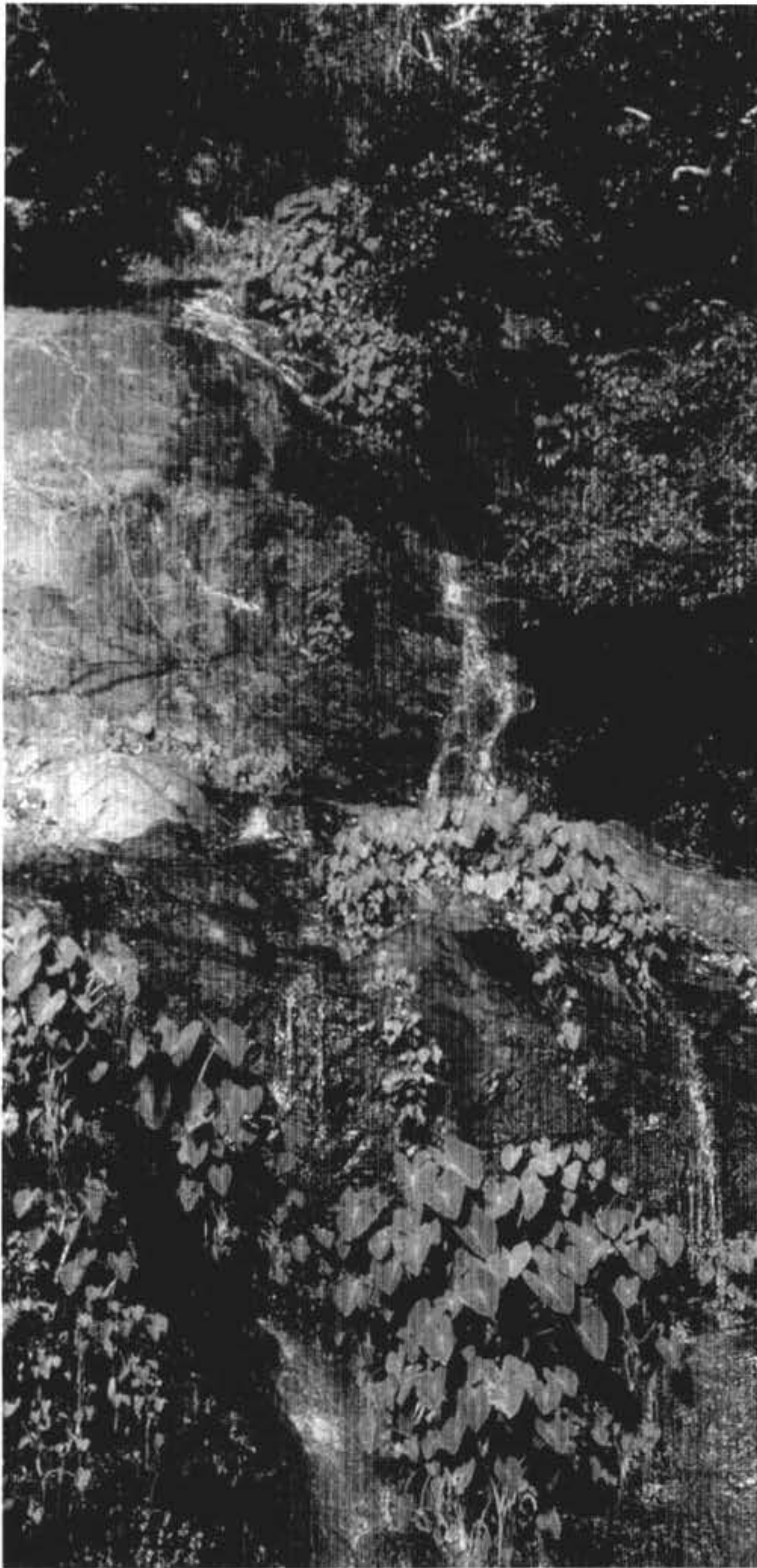


Figure 2. Isabella Falls, Queensland, a typical habitat for wildtype taro, and collection site for *Tarophagus* sp. (4th August 1992) (site 4, near Cairns, Fig.1).

thoppers were mostly seen on the undersides of fully emerged leaf blades. They were also seen on the upper petioles of heavily infested leaves. Adults are 2–3 mm long. When a leaf was turned over gently, adults and juveniles sometimes walked with a sideways or diagonal motion across the leaf surface. When disturbed by a jolt to the leaf, the escape response was a sudden large jump, away from the plant. To collect planthoppers, I used a 1.5 ml plastic Eppendorf tube containing a small twist of tissue paper impregnated with two or three drops of chloro-

form. The insects were easily approached with the tube, and were quickly overcome by the chloroform vapour. One tube could be used repeatedly without closing the lid. The tubes were posted to Canberra for cold storage.

All *Tarophagus* specimens were collected from what is now regarded as wildtype taro, a wild form of taro with long stolons, entirely green leaves, and extreme acidity (Matthews 1997). Specimens from eight different sites (localities) were sent to M. J. Fletcher and are now lodged in the entomology collection of the NSW Agricultural Scientific Collections Unit (ASCU), Orange.

#### *Identification and location records*

Two specimens were identified for the author as *T. colocasiae*, by J. F. Donaldson (from the Russell River site, 1987) and by M. J. Fletcher (from one of the 1992 samples and sites, sample not identified). Various juvenile and adult forms were seen, but were not studied in detail. Samples from six of eight sites included short-winged adults (Cooper Creek tributary; Saltwater Creek; South Mossman River crossing; Isabella Falls; Kearney's Falls; and Zillie Falls) (M. J. Fletcher pers. comm. 2001). A nymph of *Tarophagus* sp. is shown in Fig. 3, and an adult of *T. colocasiae* is shown in Fig. 4. It is difficult to identify nymphs because the taxonomic descriptions for *Tarophagus* species are based on adult morphology (J. F. Donaldson, pers. comm. 1987).

*Tarophagus* sites recorded by the author in Queensland are mapped in Fig. 1 and described in Table 1. The twelve sites span large distances from north to south and west to east, but represent only a small fraction of the full range of wild taros in Queensland and Northern Territory (see Fig. 1, and Matthews 1990, 1991). In Fig. 1, the lack of recorded *Tarophagus* at a wild taro site does not imply absence, for I did not always look for insects and the time spent at some sites was very brief. In other words, the search for insects was more opportunistic than systematic.

Additional records have been provided by J. F. Donaldson (pers. comm. 2001):

#### *T. colocasiae*

- i. on taro, Darnley Island, Torres Strait (J. F. Donaldson, 29 March 1990)
- ii. on taro, Bamaga, Qld (J. W. Turner, 28 February 1999)

#### *T. persephone*

- iii at light, Iron Range, Qld (R. J. Houston, 13–20 May 1995)
- iv on *Mimosa pigra*, Berrimah, NT (C. Wilson, 25 September 1989)
- v on *Sida cordifolia*, Fogg Dam, NT (C. Wilson, 3 April 1985)
- vi in light trap in *Mimosa pigra*, C.P.R.S., NT (C. Wilson, 4 October 1988).



#	Identification	Location	Approx. latitude S. & longitude E.	Collector & date
1	<i>T. colocasiae</i> (J.D.)	Jiyer Cave, Russell River	17° 26' 147° 47'	Matthews 20.9.87
2	<i>Tarophagus</i> sp. (J.D.)	Moochoopa Falls, upper Russell R.	17° 25' 145° 47'	Hinxman 8.10.89
3	<i>Tarophagus</i> sp. (P.J.M.)	Milmilgee Falls, Freshwater Creek	16° 58' 145° 40'	Matthews 2.8.92
4	<i>Tarophagus</i> sp. (P.J.M.)	Isabella Falls, Isley Hills	17° 02' 145° 43'	Matthews 4.8.92
5	<i>Tarophagus</i> sp. (P.J.M.)	Kearney's Falls, Bellenden Ker N.P.	17° 04' 145° 47'	Matthews 5.8.92
6	<i>Tarophagus</i> sp. (P.J.M.)	Elinjaa Falls, Atherton Tableland	17° 30' 145° 39'	Matthews 5.8.92
7	<i>Tarophagus</i> sp. (P.J.M.)	Zillie Falls, Atherton Tableland	17° 29' 145° 39'	Matthews 5.8.92
8	<i>Tarophagus</i> sp. (P.J.M.)	Saltwater Creek, vic. Mossman	16° 24' 145° 22'	Matthews 7.8.92
9	<i>Tarophagus</i> sp. (P.J.M.)	Cooper Creek trib., vic. Cape Trib'n N.P.	16° 11' 145° 25'	Matthews 7.8.92
10	<i>Tarophagus</i> sp. (P.J.M.)	Stewart Creek, Daintree R. trib.	16° 16' 145° 19'	Matthews 8.8.92
11	<i>Tarophagus</i> sp. (P.J.M.)	Martin's Ck Falls, Daintree R. trib.	16° 15' 145° 18'	Matthews 8.8.92
12	<i>Tarophagus</i> sp. (P.J.M.)	S. Mossman River crossing, Cook Hwy	16° 29' 145° 24'	Matthews 9.8.92

Table 1. Records of *T. colocasiae* and *Tarophagus* sp. in Northeast Queensland, 1987–1992. Numbers (#) refer to the sites numbered in Fig. 1.

I note that the plants *Mimosa pigra* and *Sida cordifolia* are both major introduced weeds in northern Australia. Neither species is likely to be a true host for *Tarophagus*. The insects may have been collected on or near taro in habitats that were invaded with weeds.

#### *The habitats of wildtype taro*

In Queensland there are many stable populations of wildtype taro in and around waterfalls, where rocky crevices allow strong root-holds. Taro was also found on soft banks next to fast streams or rivers, habitats that are unstable because of erosion during periods of heavy water flow (Matthews 1995, 1997). Stable taro populations in slow water courses were more common in the lowlands in the recent past, within the living memory of local observers. Sugarcane farmers at Ingham (1987 survey) and near Edmonton (1992 survey) reported that wild taros were more abundant in the lowlands when fewer swamps had been drained and cleared for sugar-

cane cultivation. Next, two sites are described in detail in order to show how habitats varied.

One of the most isolated sites visited was Jiyer Cave, next to the Russell River (site 1, Table 2 and Fig. 1). Here, wildtype taro plants were abundant and firmly established by roots and stolons among rocks below a small waterfall, deep in rainforest. *Alocasia* sp. (presumably *A. brisbanensis* Hay and Wise 1991) was also present in a drier situation nearby. Isolated clumps of taro of the same phenotype were also seen on bends of the river within a few km below Jiyer Cave. One isolated clump of an apparently escaped cultivar, with red colouring on the petiole, was also seen opposite the site of a former Chinese gold-panners' camp on the river, also a few kilometers downstream from the cave. Jiyer Cave has been the site of archaeological excavations showing late Holocene occupation (Horsfall 1996), and was still used as a campsite by Aborigines in the early 20th century, and by recreational visitors to Bellenden Ker National Park in recent years.

One of the least isolated sites found was on a bank of the South Mossman River, at its intersection with the



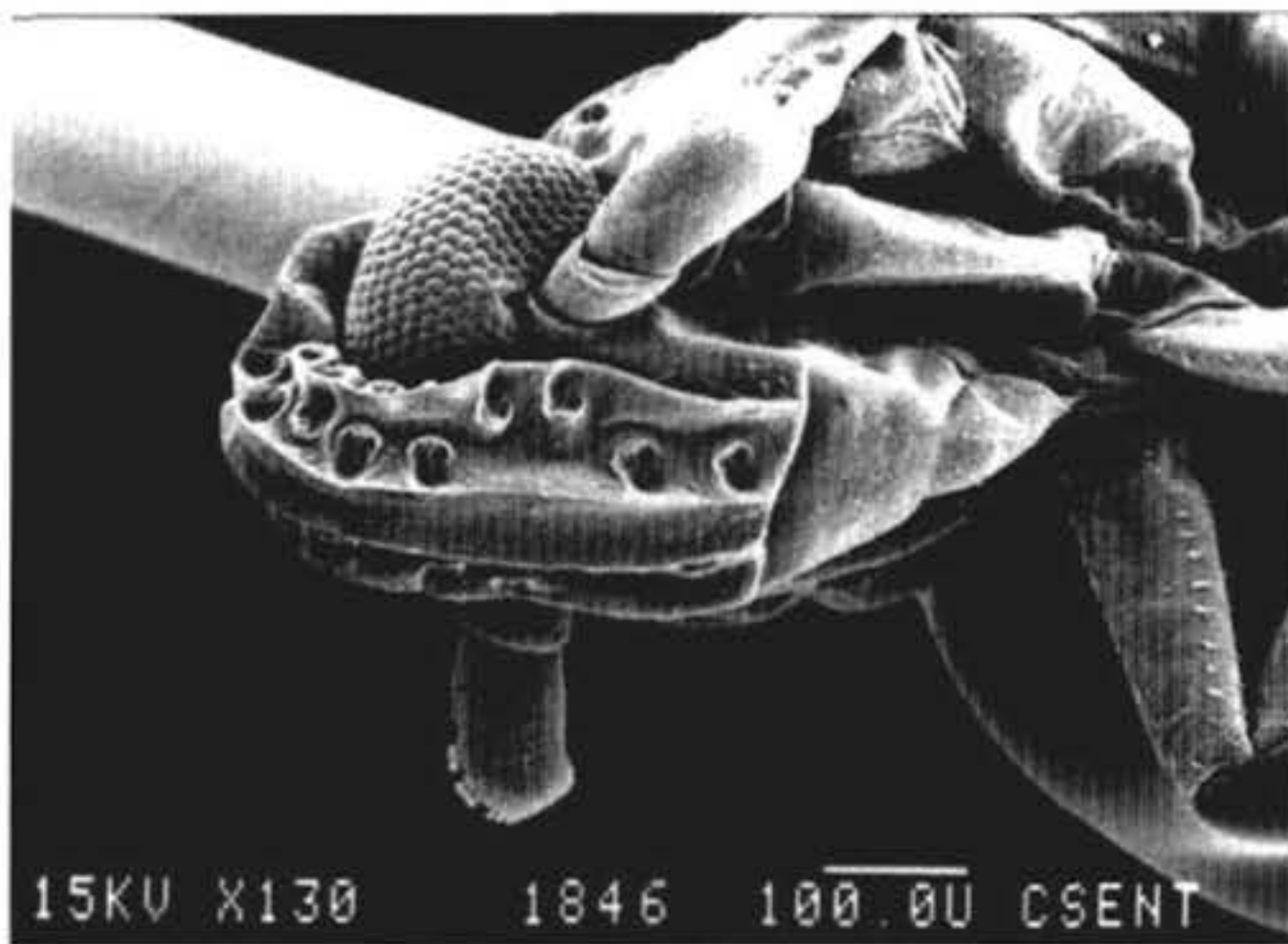
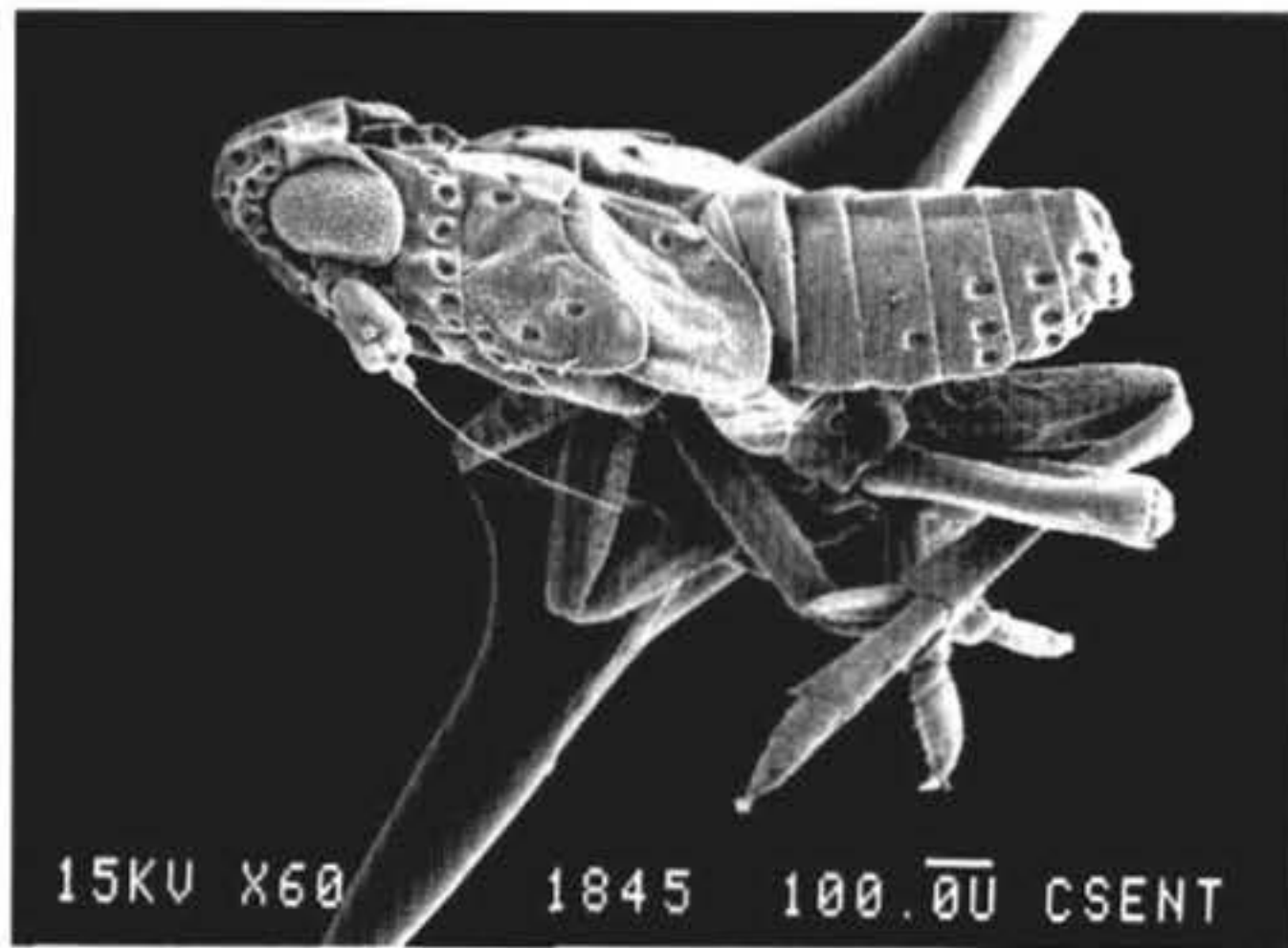


Figure 3. Nymph of *Tarophagus* sp. from a leaf of wild taro collected by R. Hinxman, 8th October 1989, in rain-forest at Moochoopa Falls, Bellenden Ker National Park, Northeast Queensland. Upper photo: whole body. Lower photo: front of head. Scale bars 100  $\mu$ m (0.1 mm) in both photos. The antennae, head structure, number of abdominal plates, and foliate spur on the rearmost leg appear the same as shown for the adult stage of *Tarophagus*, in Asche and Wilson (1989a,b). Photographed with a Joebel scanning electron microscope by D. Rentz.

Cook Highway. At this site, a dense patch of wildtype taro grew in soft mud and accumulated detritus, beneath a remnant of riparian broadleaf rainforest. This remnant of forest was surrounded by sugarcane fields.

#### *Taro and insects in Australia*

During the fieldwork in Queensland, I also tried to find pollinating insects like those seen on taro in Papua New Guinea, in 1985. None were found, despite the fact that fruiting heads with many seeds were present. The presence of seeds strongly suggested that pollination had taken place, since asexual production of seeds has not

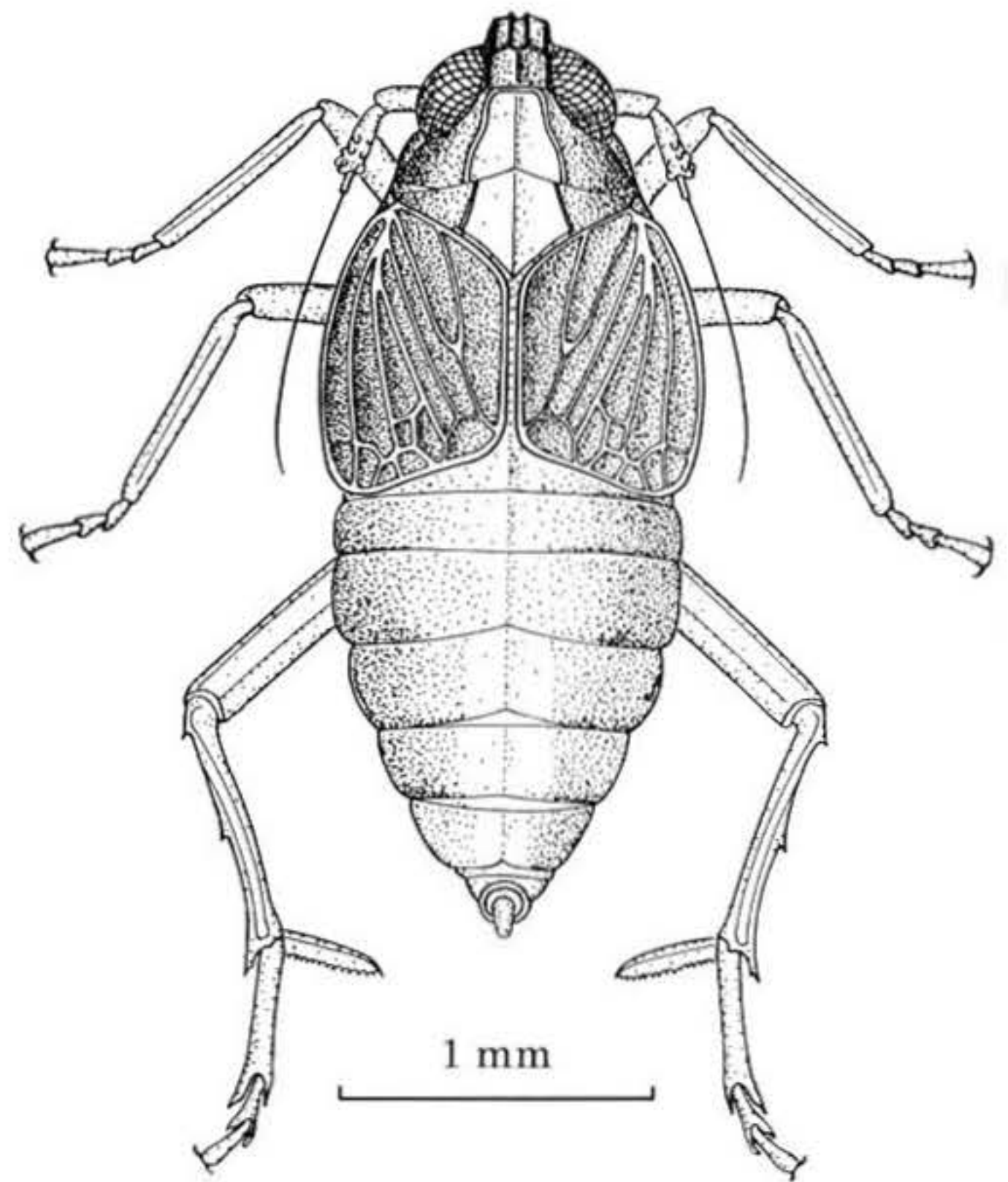


Figure 4. Dorsal view of *Tarophagus colocasiae* (Matsumura), adult (with short wings), collected in Queensland by Matthews, August 1992. The pointed abdomen indicates that this specimen is a female. Drawing by A. Westcott, NSW Agriculture (courtesy M. J. Fletcher).

been reported in taro. Flowering dates in Queensland span at least seven months, from March (R. Hinxman, pers. comm. 1989) to October (author's field-work 1987, 1992), but the periods for individual plants or sites are not known. At any one site, drosophilid flies might visit inflorescences only briefly or sporadically. Alternatively, other pollinators may be involved, or rainfall in this area may facilitate self-pollination of the plants, as Ivancic *et al.* (1995) reported in Papua New Guinea.

Whether or not the insect pollinators and planthoppers are associated exclusively with taro is not entirely certain. Efforts to find these insects on other plants, in wild and cultivated habitats, are needed to properly test the limits of host-range for each insect species. The known geographical distributions of the three *Tarophagus* species overlap in the eastern part of mainland New Guinea (Figure 5), so this might be a key area for investigating relationships between *Tarophagus* species and their plant hosts.

Most of the *Tarophagus* sites in Northeast Queensland were isolated with respect to human settlement and/or taro cultivation. Taro cultivars and cultivation are said to have been introduced from the Pacific Islands by labourers employed in the sugarcane industry during the 19th century, and taro is still occasionally



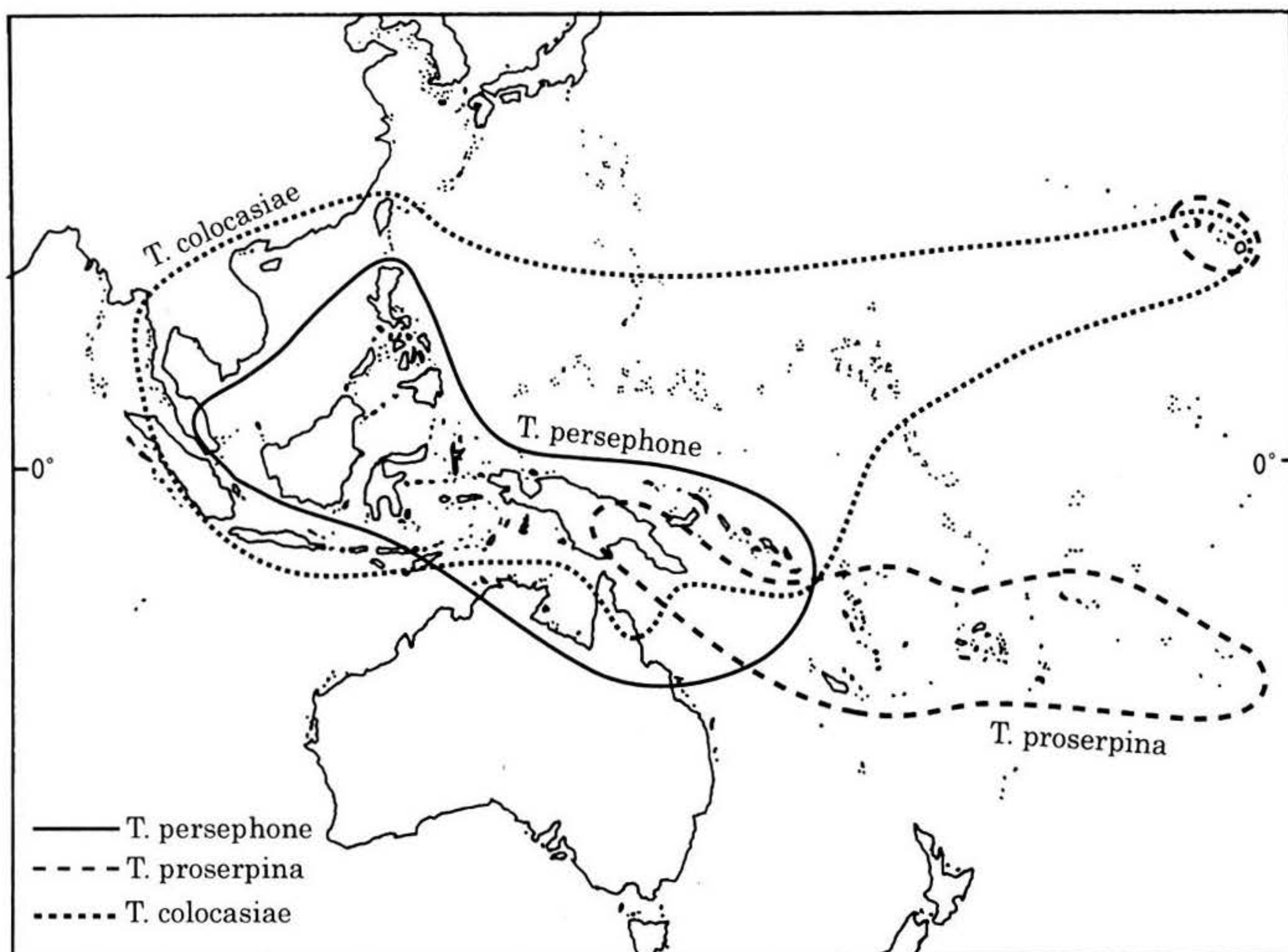


Figure 5. *Tarophagus* species, distribution map, adapted from Asche and Wilson (1989a,b) with the addition of *T. colocasiae* in Queensland.

replanted by their descendants, in valleys behind the Gold Coast in South Queensland (D. E. Shaw pers. comm. 1992). For most Australians with European origins, taro is an unfamiliar food. In 1987 and 1992, when I carried out my field work, taro was rarely grown as a commercial crop in Australia. In Queensland, a few growers had started or were planning commercial production, and small quantities of fresh taro were sold in vegetable shops in Mossman and Cairns. In 1992 I was told that Vietnamese market-gardeners had started growing taro near Darwin within the last five years, but that there was still no more than a 1/4 acre of taro grown in all of the Northern Territory. Commercial production in Australia has increased during the last ten years, judging from recent conversations with vegetable sellers in Sydney, but most taro consumed in Australia is still imported. The general lack of taro cultivation in Australia makes it likely, though not certain, that the association of taro planthoppers with wild taro in Queensland is prehistoric, and not just the result of modern introduction on taro cultivars.

#### *Taro planthoppers and viruses in Melanesia*

Mitchell and Maddison (1983) listed *Alocasia* as an alternative host for *T. proserpina*, but gave no source for this information. It is also unlikely that these authors made any distinction between what are now recognised as three species of *Tarophagus*. Asche and Wilson (1989a) noted that *Tarophagus* species are found on taro, but made no direct claims concerning host specificity. Gagné (1982) is perhaps most explicit, stating that the entire life history of the taro leafhopper occurs on taro stems, and reporting other hosts for other pests of taro, but not for *Tarophagus*.

Despite some uncertainty, the existing literature does indicate that taro is the sole host for *Tarophagus*, so it is of historical interest to consider *Tarophagus* as a host or vector for other forms of life. Asche and Wilson (1989a, b) discuss a mirid egg predator (*Cyrtorhinus fulvus* Knight) that attacks *Tarophagus*, and here I will discuss viruses transmitted by *Tarophagus* to taro.

Taro bobone virus is apparently endemic to Papua



New Guinea and the Solomon Islands (Mitchell and Maddison 1983), although it is part of a poorly defined complex of viruses or virus strains that is more widely distributed in the Pacific (Pearson *et al.* 1999, Jackson 1994). This virus has not been reported in taro in Australia, with the exception of imported material held in quarantine (Jones *et al.* 1980). According to a 1990 revision by Brunt, in Brunt *et al.* (1996), taro bobone virus is transmitted by *T. proserpina* in a persistent manner, and is not transmitted by mechanical inoculation, by contact between plants, by seed, or by pollen. The host range of taro bobone virus also appears to be limited to taro: no natural infection of this virus has been recorded in *Alocasia* or *Cyrtosperma* (aroids native to tropical Asia and the Pacific) or *Caladium* and *Xanthosoma* (aroids native to Central and South America, and now common in Asia and the Pacific).

*Tarophagus* is the only insect genus known to transmit taro bobone virus, but the identification of *T. proserpina* as vector cannot be relied upon since it was made before the 1989 revision of the genus. Although taro bobone virus has been reported in both Papua New Guinea and the Solomon Islands, Asche and Wilson (1989a) express surprise that they did not find *T. proserpina* in the Solomon Islands. If this species really is absent, then taro bobone virus may exist in the Solomon Islands because it was introduced in vegetative planting materials, and/or because it is transmitted by *T. colocasiae* or *T. persephone* (both present in the Solomon Islands). For agricultural researchers, vegetative transmission of taro bobone virus is considered a high risk, and this has discouraged the export of cultivars from Papua New Guinea and the Solomon Islands (Jackson 1994).

The apparent severity of taro bobone virus in Papua New Guinea and the Solomon Islands might mean that taro in this area was previously unexposed, and was therefore especially susceptible to recent introduction of the virus. In theory, the virus could exist undetected in other regions, in resistant forms of taro. Alien pathogens are often involved in the most severe diseases of plants (Scheffer 1997). Alternatively, taro bobone virus might have emerged locally from the complex of rhabdoviruses or rhabdovirus strains (see Pearson *et al.* 1999) that is wide-spread in Micronesia and Melanesia. From current evidence, it is not possible to say when or where taro bobone virus originated. Nevertheless, if taro is the only host for the rhabdovirus complex, and if *Tarophagus* is the only vector, then the overall association of viruses, plant, and insects may be ancient, in Melanesia or elsewhere. Unraveling the history of this association is likely to shed light on the domestication and dispersal of taro.

Another virus, Dasheen Mosaic Virus (DMV), is common worldwide among cultivated aroids (Zettler and Hartman 1986), is transmitted by aphids, and is not restricted to taro as a host. Greber and Shaw (1986) found DMV in Queensland in various cultivated specimens of *Alocasia*, *Colocasia*, *Dieffenbachia*, and *Xanthosoma*, and also in wild *Alocasia macrorrhizos* (presumably *A. brisbanensis* Hay and Wise 1991) at

three locations in rainforest. During my own field work, I did not observe symptoms of any viruses among wild taros in Queensland, but this does not exclude the possibility that symptomless strains of virus were present.

Much remains to be learned about the viruses associated with taro, and their historical significance is not yet clear. Characterisation of the viruses is being carried out by Pearson and others (Pearson *et al.* 1999).

#### *Biogeography of the taro planthopper and taro*

Asche and Wilson (1989a, b) did not report *Tarophagus* in India and adjacent countries (Fig. 5), despite the fact that wildtype and domesticated taros and other species of *Colocasia* are found in Northeast India and adjacent areas (Matthews 1991, 1995, 1997). *T. colocasiae* and/or undescribed species of *Tarophagus* might exist in these areas. Reviewing local research literature from India and adjacent areas might help to define the western limits of *Tarophagus* more securely. In this section, I briefly review the biogeography of each *Tarophagus* species in Southeast Asia and the Pacific, with reference to taro and its dispersal as a cultivated plant.

(1) *T. colocasiae* is the most widespread species, ranging from the Asian mainland, through Indonesia and the Philippines to Micronesia, Australia, New Guinea, Solomon Islands, and Hawaii (Fig. 5). According to Waterhouse and Norris (1987), *Tarophagus* was first established in Hawaii in 1930, when its population rose and caused major crop damage. It is not known if this statement is supported by any definite evidence. Perhaps *Tarophagus* was introduced at an earlier date (pre-European), but only became obvious as a pest because of special environmental circumstances. Today, both *T. colocasiae* or *T. proserpina* are found in Hawaii, and the latter is apparently more abundant (Asche and Wilson 1989b). *T. colocasiae* might have been introduced to Hawaii from China or southernmost Japan, on taro cultivars brought by Chinese or Japanese immigrants during the late 19th and early 20th century. There might also have been an earlier dispersal eastward, on cultivated taros carried from Southeast Asia and/or New Guinea, into Micronesia and possibly as far as Hawaii. Whatever the dispersal history may be, *T. colocasiae* may have a more western origin than the other planthopper species, since it is the only species known to be widespread in the Asian mainland.

(2) *T. persephone* has been found in island Southeast Asia, North Australia, and Melanesia, but not in New Caledonia, Micronesia, Sumatra, Java, and most of mainland Southeast Asia. Asche and Wilson (1989a:294) argued that *T. colocasiae* and *T. proserpina* are sister species. This makes the more central geographical position of *T. persephone* (Fig. 3) rather curious — why is it not more closely related to one or the other species? *T. persephone* could have originated on either side of Wallacea, or within Wallacea, in a primary association with natural, wild populations of taro, or possibly in a



primary association with *Colocasia oreshia* and/or *C. gigantea*. These two species are native to Southeast Asia (Hay 1996), in areas that overlap or lie within the currently known range of *T. persephone*. Speculating about the original distribution and associations of *T. persephone* is difficult because nothing is known about the occurrence of planthoppers on other species of *Colocasia*, or on natural, wild populations of taro in any part of Southeast Asia and Melanesia.

(3) *T. proserpina* is present in the eastern part of Papua New Guinea, but has not been reported in the arc of islands from New Britain to New Ireland and the Solomon Islands. From eastern Papua New Guinea, this species is found eastward through Vanuatu, New Caledonia, and across the southern Pacific islands to the Society group, and also in Hawaii. As indicated above, an early (pre-European) arrival of *Tarophagus* in Hawaii may be in doubt, since it has been suggested that the genus was established in there in 1930. Nevertheless, the apparent abundance of *T. proserpina* in Hawaii (Asche and Wilson 1989b) might reflect early establishment there, before a more recent arrival of *T. colocasiae*. *T. proserpina* has also been found in the Society Islands, on Raiatea in 1927 (Gillespie *et al.* 2000) and recently on Moorea (G. R. Roderick pers. comm. 2001). The apparent absence of *Tarophagus* throughout a very large area of central Polynesia may reflect a lack of investigation, and also the presence of many small and isolated islands with little or no taro. On such islands, *Tarophagus* might have been present never or intermittently.

#### *Origins of taro in Oceania*

From west to east, there may have been two general routes for the early movement of taro and taro planthoppers: (i) a northern route taking *T. colocasiae* into Melanesia, Micronesia, and possibly Polynesia (from Sunda to Sahul and to Near Oceania and Remote Oceania), and (ii) a southern route carrying *T. proserpina* into Remote Oceania. The distribution of *T. proserpina* is especially intriguing because it is apparently absent in East Asia, Southeast Asia, Micronesia, and Australia. Since all three species are sympatric in the mainland of Papua New Guinea (Fig. 5), *T. proserpina* apparently can coexist with other *Tarophagus* species, though not necessarily on the same plants or in the same habitats. Asche and Wilson (1989a:294) found no morphological evidence for hybrid belts or clines. The western limits of *T. proserpina* might reflect natural and agricultural processes: limited flying ability, limited ability to coexist with other planthopper species on plants or in habitats, and limited transfer of planting materials westward or northward. As explained later, taro planthoppers are easily carried on planting materials.

In Polynesia, taro is believed to be an entirely exotic plant, introduced by humans. The eastward movement of *T. proserpina*, into Polynesia, may be largely due to

transport on planting materials, followed by establishment in taro gardens. Although the exact eastern limits of natural populations of wildtype taro are not yet known, the known distribution of *T. proserpina* may point to eastern mainland New Guinea as a locus for the domestication of taro within New Guinea, and as a geographical source for cultivars in Polynesia.

The above suggestions are all very tentative. Whether or not they are credible will depend on many as yet unknown details of plant and insect distribution. For example, we need to know much more about how taro planthoppers migrate, in wild and cultivated habitats. According to Anon (1999a), *T. proserpina* lays eggs, often two at a time, into slots cut with the ovipositor, in the midrib of the taro leaf and also in the petioles and petiole bases. The latter are a major source of infestation for new gardens since propagation is by means of corm tops with petiole bases. In Hawaii the duration of the egg stage averages about 14 days and that of the five successive nymphal instars about 4, 3, 3, 4, and 5 days. These observations have two implications: (i) the planting materials carried on long-distance canoes must have included corms with attached petioles, if not entire plants with full leaves, and (ii) taro planthoppers could survive long journeys as unhatched or juvenile forms inside their host, or on their host and protected by surrounding leaves or packing materials.

In tropical Asia and the Pacific, and other tropical regions, taro cultivars are very commonly propagated using corms (or corm tops) with petioles (leaf stalks) attached and the blades removed. In contrast, most temperate cultivars are propagated using small side-corms that lie dormant and leafless during winter. Removing the blades reduces water stress for the plant, and would not prevent the transport of taro planthoppers. As a quarantine measure to prevent the transport of planthoppers with planting materials, Zettler *et al.* (1989) recommended removing the sheathing petiole bases until they are free of signs of feeding or egg-laying punctures. Anon (1999b) stated (in relation to *T. persephone*) that most adult planthoppers produced cannot fly, so that using clean planting stock is a 'useful weapon' in preventing the spread of planthoppers to new plantings. Then follows a lament that 'all too often in traditional plantings it is not possible to have this recommendation implemented'. The recommendations cited here suggest that very deliberate and unusual actions would have been needed to prevent the spread of taro planthoppers with taro, during canoe voyages in the past. Planting materials like those common today undoubtedly permitted incidental and unintentional transport of planthoppers.

Elsewhere (Matthews 2002) I have argued that to store taro during voyages, for later planting, special care might have been taken to maximise the number of healthy buds and growing shoots. Special care may have included (i) prevention of skin damage during harvest and transport, by not breaking mother corms and side-shoots apart, and by wrapping them in clean materials, and (ii) use of wrapping materials and on-board locations



that provided the best possible conditions of temperature, moisture, and aeration. Although there is no reason to assume that special care was always necessary or attempted, there may have been attempts to maximise the survival of plants during long voyages of unknown duration. Wrapping ordinary taro planting materials with leaves or other materials, in bags or baskets, would have helped reduce exposure and water loss. An incidental result of wrapping may have been to improve the survival of planthopper eggs, juveniles, and adults. If whole taro plants were transported with corms, roots, and leaves intact, then water loss from the leaves would have been a problem. To prevent dehydration and root damage, the whole plant could have been wrapped in some way, with the corms and roots kept in damp soil or humus. Such transport might have maximised chances for the transfer of juvenile and adult forms of *Tarophagus*, on leaf blades and petioles, as well as maximising chances for the transfer of other organisms closely associated with taro, e.g. land snails (Kirch *et al.* 1992).

#### ***Tarophagus* species and taro gene pools**

Previously, various lines of evidence led me to propose that indigenous selection and domestication of taro occurred over a wide geographical range, and involved genotypically and phenotypically diverse natural wild forms of taro (Matthews 1990). At that time, the genetic data was still weak. Since then, isozyme variation has been surveyed in many wild and cultivated forms of taro, across Asia and the Pacific. Lebot and his colleagues reported two distinct taro gene pools in Southeast Asia and Melanesia, and proposed that these reflect natural differentiation of the species on each side of the Wallace Line (Lebot and Aradhya 1991, Lebot 1999, Lebot *et al.* 2002). These authors also reported very little genetic diversity among Polynesian taros, and suggested that Polynesian taros are derived from the larger Melanesian gene pool. Tahara *et al.* (1999) found two distinct taro gene pools in Nepal and Yunnan (South China). In sum, these studies suggest the possibility that each species of *Tarophagus* evolved in association with a different natural taro gene pool, before the domestication of taro in multiple locations or regions.

If the distribution of *T. colocasiae* actually extends further west than shown in Fig. 5, then this species might have originated in association with taro in the Asian mainland. *T. persephone* might have originated in island Southeast Asia or Melanesia, and *T. proserpina* in Melanesia. These suggested origins and the present overlapping distributions of *Tarophagus* species must somehow reflect past dispersals of wild and cultivated taros, but little more can be said until we know more about planthopper populations and migration in wild and cultivated habitats. Matthews (1997) reported that wildtype taros exist in both stable and unstable habitats. Investigating the planthoppers in these habitats could be

useful, since planthopper migration is likely to vary according to habitat persistence (cf. Denno *et al.* 1991).

Within Australia (Fig. 5), the reports made so far indicate that *T. persephone* and *T. colocasiae* are not uniformly distributed across northern Australia. This is intriguing because different patterns of ribosomal DNA were previously found in wildtype taros from Western Australia, Northern Territory, and Queensland (Matthews and Terauchi 1994). If different planthoppers are closely associated with different lineages of wildtype taro, then dispersal of the insects may have been closely linked with dispersal of the plants.

#### **Conclusions**

For historical purposes, the present observations of *Tarophagus* in Queensland may be most significant because (i) they demonstrate a close association of the insect with wildtype taro, for the first time, and (ii) only *T. colocasiae* was found, thus making it more likely that *T. proserpina* is restricted to New Guinea. The present observations are also significant for agricultural ecology: the abundance and wide geographical range of *Tarophagus* in Queensland suggests that taro bobone virus, or similar insect-transmitted viruses, could spread quickly among wild and/or cultivated taros, if the viruses are introduced. Many areas of Queensland are very suitable for growing taro, and interest in the crop is increasing. It would be unfortunate if natural populations of *Tarophagus* and its host were to become the targets of agricultural pest control.

*Tarophagus* is of special historical interest because it has a very close relationship with taro, a crop that has been central to interpretations of archaeological evidence for early agriculture in New Guinea (Golson and Hughes 1980, Bayliss-Smith and Golson 1992). The present evidence and interpretations also highlight New Guinea, and especially eastern New Guinea, as a possible locus for the domestication of taro, and as a likely origin for taro in much of Oceania.

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