

CHAPTER  
18**Biological Control of the Cycad Aulacaspis Scale,  
*Aulacaspis yasumatsui*****Ronald D. Cave<sup>1</sup>, Aubrey Moore<sup>2</sup>, and Mark Wright<sup>3</sup>**<sup>1</sup>Indian River Research and Education Center, Institute of Food and Agricultural Sciences, University of Florida, Ft. Pierce FL [rdcave@ufl.edu](mailto:rdcave@ufl.edu)<sup>2</sup>College of Natural and Applied Sciences, University of Guam, Mangilao GU [aubreymoore@triton.uog.edu](mailto:aubreymoore@triton.uog.edu)<sup>3</sup>Department of Plant and Environmental Protection Sciences, University of Hawaii at Mānoa, Honolulu HI [markwrig@hawaii.edu](mailto:markwrig@hawaii.edu)**NON-TECHNICAL SUMMARY**

The cycad aulacaspis scale, *Aulacaspis yasumatsui* (Hemiptera: Diaspididae), is a worldwide pest of cycads. In Florida, Hawaii, and elsewhere, cycads are used as urban landscape plants and exported for sale as potted plants. The scale has decimated the cycad production industry and reduced the use of the king sago palm, *Cycas revoluta*, and other cycads as ornamental plants. On western Pacific islands, the scale is destroying populations of native *Cycas micronesica* in natural habitats. The invasion of Guam by the cycad aulacaspis scale has led to the death of at least 90% of the island's *C. micronesica* trees. The parasitic wasp *Coccobius fulvus* (Hymenoptera: Aphelinidae) and the predatory beetle *Cybocephalus nipponicus* (Coleoptera: Cybocephalidae) were released in Florida and became established but did not provide satisfactory control of the pest. The parasitic wasp *Arrhenophagus chionaspidis* (Hymenoptera: Encyrtidae) was first detected attacking cycad aulacaspis scales in Florida in 2012, but its influence on pest populations has not been evaluated. In Hawaii, the lady beetle *Rhyzobius lophanthae* (Coleoptera: Coccinellidae) seems to be a good biological control agent as it can be effective under a range of conditions. The parasitoid wasp *Aphytis lingnanensis* (Hymenoptera: Aphelinidae), or a cryptic species very similar to it, may have a significant effect on cycad aulacaspis scale populations in Hawaii, where infested plants seem to survive the presence of the scale insect when the parasitoid causes high levels of scale mortality. *Rhyzobius lophanthae* was introduced to Guam and is established but does not protect young cycads. *Arrhenophagus chionaspidis* occurs in Guam and appears to cause high rates of parasitism on the leaves. Attempts to introduce *C. fulvus* and the Hawaiian *Aphytis* species to Guam were unsuccessful. Exploration in Asia discovered a lady beetle, *Phaenochilus kashaya* (Coleoptera: Coccinellidae), which may be an effective biological control agent, but currently there are no plans to introduce this predator to western Pacific islands. Introductions of an *Aphytis* species from Hawaii and *C. nipponicus* from Florida may offer hope of saving the native *C. micronesica* in Micronesia.

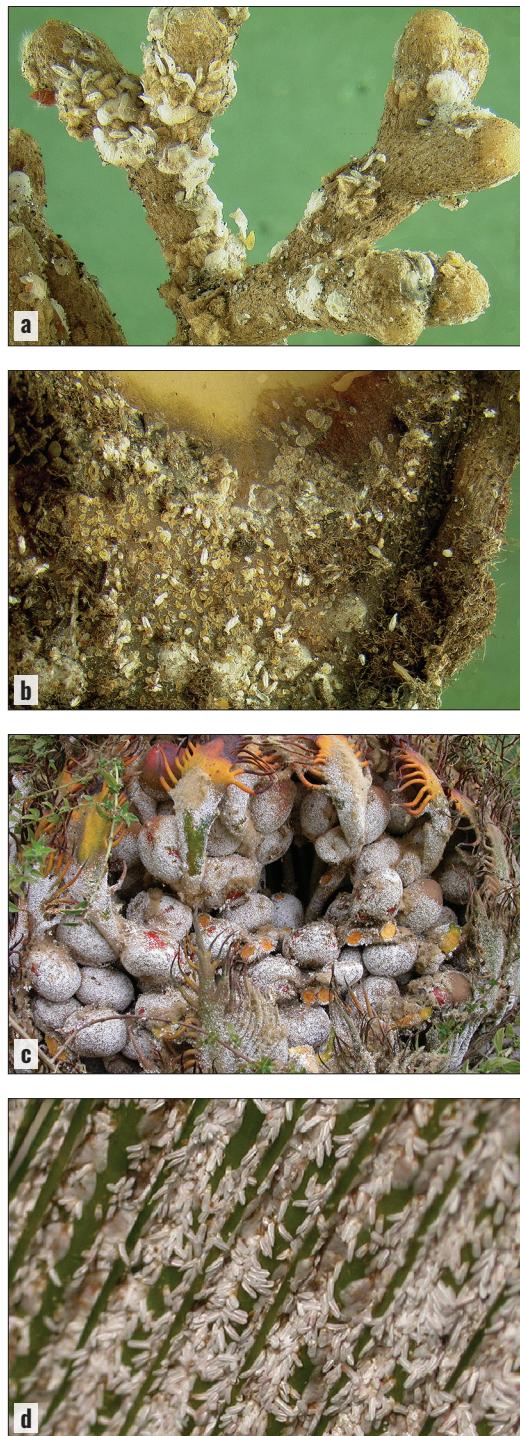
## HISTORY OF INVASION AND NATURE OF PROBLEM

### The Species Invasion

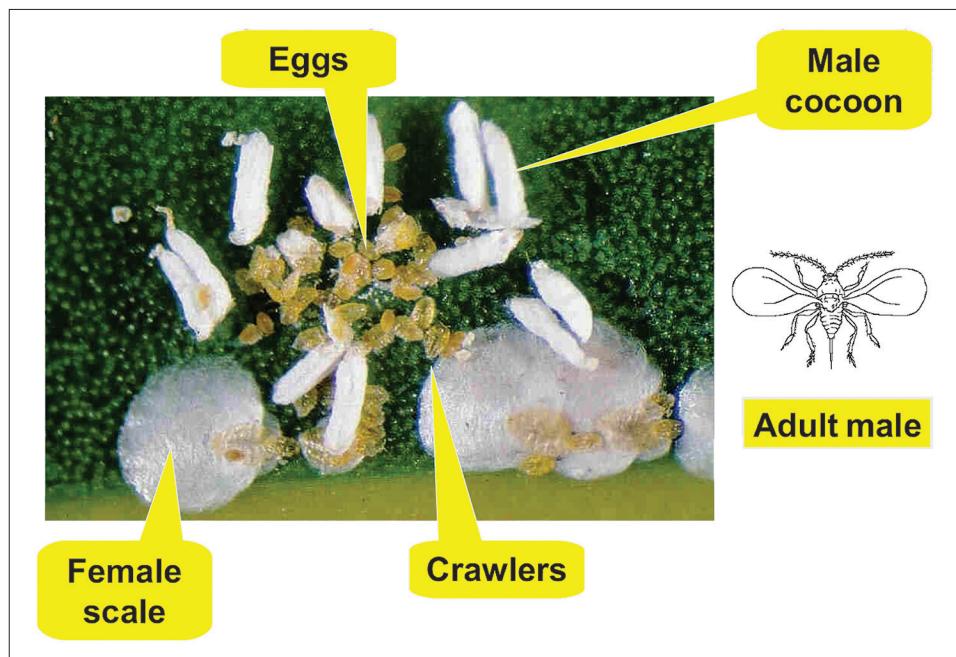
The cycad aulacaspis scale, *Aulacaspis yasumatsui* (Hemiptera: Diaspididae), was discovered infesting cycads in 1994 in the Montgomery Botanical Center in southern Florida, after it was unknowingly brought to the Center on infested plants from Southeast Asia (Tang et al., 2006), where it is native (Takagi, 1977). Infestations of the scale were particularly severe on *Cycas* spp. and *Stangeria eriopus* (a South African cycad in a monotypic genus). From this single infestation point, the scale spread throughout Florida and into other southeastern U.S. states and Texas. Hawaii became infested with the cycad aulacaspis scale by 1998, when the pest was detected on Oahu, and the scale has subsequently been found on the islands of Hawai'i and Kaua'i (Heu et al., 2003). The scale was found in Guam in 2003 on ornamental king sago palms (*Cycas revoluta*) (Terry and Marler, 2005). Within two years, the scale spread through most of Guam and invaded the native forests of *Cycas micronesica*, an indigenous tree unique to Micronesia (Moore et al., 2005a). The pest was discovered on Rota in 2007 (Calonje, 2008) and Palau in 2008 (Orapa and Cave, 2010). Cycad aulacaspis scale is now established in many tropical and subtropical regions and countries, including the West Indies, Mesoamerica, Indonesia, Singapore, Philippines, China, Vietnam, Micronesia, Africa, and southern Europe (Howard et al., 1999; Weissling et al., 1999; Hodgson and Martin, 2001; Moore et al., 2005a; Bográn et al., 2006; Germain and Hodges, 2007; Segarra-Carmona and Pérez-Padilla, 2007; Marler, 2012; Muniappan et al., 2012; Normark et al., 2017; Dimkpa et al., 2021; Macharia et al., 2021; Marler et al., 2021). The dispersal route responsible for this broad distribution is the international commercial movement of whole cycad plants, but private collectors may be another pathway for spread. The presence of cycad aulacaspis scales on the leaves is easily visible, but the insect can infest the coraloid roots (Fig. 1a), excised leaf bases on trunks, and cataphylls covered by tomentum (Fig. 1b), where they are difficult for phytosanitary inspectors to detect (Marler and Moore, 2010).

### Nature of the Problem

The sessile adult female scale creates a round, white armor under which it feeds with piercing-sucking mouthparts and lays eggs (Fig. 2). From the eggs emerge tiny nymphs, called crawlers (Fig. 2), that have functional legs but initially do not feed. The crawlers walk to other plant parts or adjacent host plants or may



**Figure 1.** Cycad aulacaspis scale, *Aulacaspis yasumatsui*, on the (a) coralloid roots, (b) cataphyll, (c) seeds, and (d) leaves of *Cycas revoluta*. (a-d: R. D. Cave, University of Florida)



**Figure 2.** Life stages of the cycad aulacaspis scale, *Aulacaspis yasumatsui*. (Illustration by A. Moore, University of Guam)

be dispersed to other plants by the wind. When the crawler finds a suitable site on the plant, it settles, inserts its mouthparts, and molts to the next life stage, which lacks legs but has functional piercing-sucking mouthparts. During feeding, the sessile, older scales secrete substances that form the armor scale covering characteristic of the insect. The male 2<sup>nd</sup>-instar scale produces a white, three-ridged covering (Fig. 2) under which the insect molts three times and eventually emerges as a tiny adult with one pair of wings (Fig. 2) but no functional mouthparts. The 2<sup>nd</sup>-instar female secretes additional covering material but remains in place, where she molts to the wingless adult stage, mates with a mobile male, and then produces eggs to repeat the life cycle.

All plants in the family Cycadaceae and several species of Zamiaceae are hosts of the cycad aulacaspis scale (Marler et al., 2021). Uncontrolled, the scale forms dense populations on the trunk, roots, seeds (Fig. 1c), and leaves (Fig. 1d). Feeding by dense scale populations deprives the host of nutrients and weakens the plant, which may die of plant pathogen infections that healthy plants could tolerate or resist.

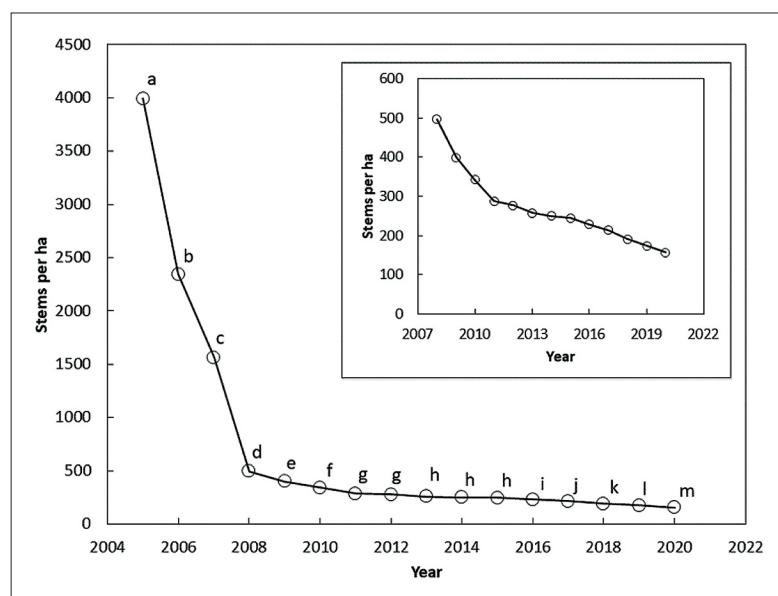
Based on an island-wide census of Guam's trees by the U.S. Forest Service in 2002, the year before the arrival of the cycad aulacaspis scale, the tree cycad *C. micronesica* was identified as the most abundant tree in Guam's forests (Donnegan et al., 2004). Within 12 years of the scale's invasion, *C. micronesica* was listed as threatened under the U.S. Endangered Species Act. Rapid decline of the *C. micronesica* population in Guam was documented by Marler and Krishnapillai (2020) (Fig. 3). Cycad stem counts declined to only 12.5% of the original number within the first three years of surveys (conducted from 2005 to 2008), and this decline continued, reaching 4% of the original count in succeeding years (2009–2020). In addition to high plant mortality, surviving cycads stopped reproducing in the research plots on Guam. The last seedling (0–10 cm [0–4 in] tall) was seen in 2006, and the last juvenile (10–100 cm [4–39 in] tall) was seen in 2014. In some areas of Guam, the mortality rate of 100-year-old *C. micronesica* trees has reached 100%.

Secondary effects of cycad aulacaspis scale on the health of *C. micronesica* are not obvious. Perhaps the most important secondary impact is much-reduced reproductive capability in plants recovering from scale infestation. Seeds from scale-infested plants are deficient in nonstructural carbohydrates, and germination rates are much lower, i.e., 43% of seeds from healthy plants germinate versus only 7% of seeds from infested plants (Marler and Cruz, 2019). In addition, Marler and Terry (2021) reported that mature male plants that

survive the initial scale infestation have significantly smaller cones than healthy plants.

Marler (2013) reported on nondestructive stem-winchng stress tests performed on *C. micronesica* trees to simulate the effects of typhoon-strength winds. Stems of plants that had not been infested by cycad aulacaspis scale were significantly stiffer than those that had been infested by the scale for either two or five years. Marler hypothesized that scale-infested plants would be more susceptible to stem failure during typhoons. Evidence supporting this hypothesis came two years later when Typhoon Dolphin passed over Guam on May 15, 2015. Marler et al. (2016) compared the level of damage from Typhoon Dolphin with that of a previous cyclone, Supertyphoon Pako, that damaged Guam's forests in 1997 when the *C. micronesica* population was healthy. Less than 2% of the healthy *C. micronesica* population exhibited wind snap damage during Supertyphoon Pako's peak winds of 298 km/h (185 mph). In contrast, Typhoon Dolphin's peak winds of only 170 km/h (106 mph) caused wind snap of 6% of Guam's unhealthy *C. micronesica* population after only 10 years of infestation by the cycad aulacaspis scale.

Cycads are highly desired by landscapers and homeowners as ornamental plants because they are long-lived, require low maintenance, and are resistant to most pests. Cycad aulacaspis scale infestations on ornamental cycads are unsightly (Fig. 4). *Cycas revoluta* (the king sago palm), the most popular ornamental cycad, is particularly susceptible to the scale. Worldwide, many ornamental king sago palms have died due to the cycad aulacaspis scale.



**Figure 3.** Number of *Cycas micronesica* stems per ha (all size categories) in 12 Guam habitats from 2005 to 2020. The inset shows results from 2008 to 2020 with a smaller vertical axis range. Ordinates of markers with the same letter are not significantly different. (from Marler and Krishnappillai, 2020, reprinted with permission)



**Figure 4.** *Cycas revoluta* with an intense infestation of the cycad aulacaspis scale, *Aulacaspis yasumatsui*. (R. D. Cave, University of Florida)

## WHY CONTROL THIS INVASIVE SPECIES?

Populations of *C. micronesica* on several island groups (Guam, the Northern Mariana Islands, and other western Pacific islands) are now threatened by the cycad aulacaspis scale (Fig. 5a,b). Currently, unhealthy

mature *C. micronesica* plants in Guam's forests are neither producing seeds (**Fig. 5d**) nor being replaced by juvenile plants (**Fig. 5c**). Without control of the invasive scale, this endemic plant, the most abundant tree in Guam's forests only two decades ago, is headed towards local extinction. Marler and Lawrence (2012) predicted the extinction of *C. micronesica* from western Guam by 2019, but small pockets of large trees still struggle to survive. There is an urgent need to control cycad aulacaspis scale so that some recovery can take place without further loss of biodiversity.

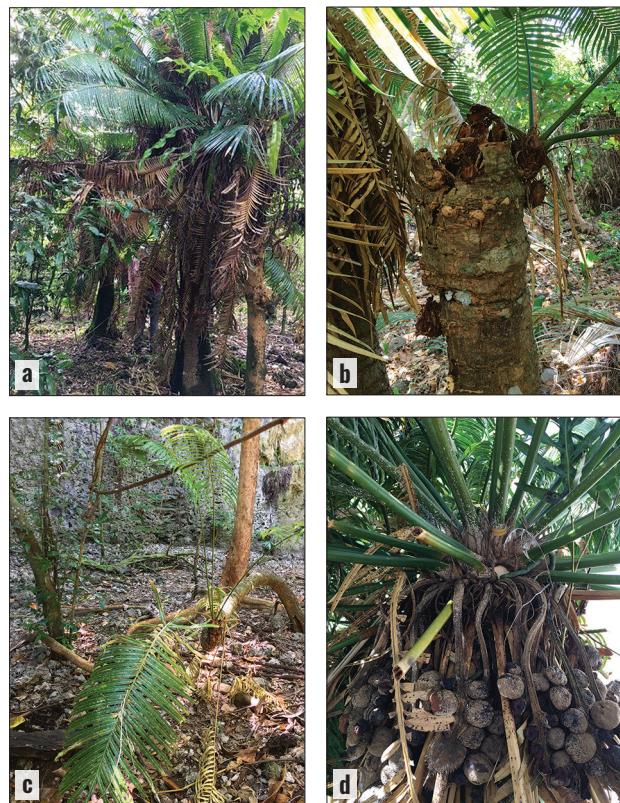
The disappearance of *C. micronesica* from Guam is likely to threaten the survival of other endangered organisms. The Mariana fruit bat, *Pteropus mariannus*, eats the fleshy, aromatic covering of *C. micronesica* seeds, which may be the bat's sole food source after a typhoon destroys less wind-tolerant fruit-bearing plants such as papaya (Haynes and Marler, 2005). In 2020, the U.S. Fish and Wildlife Service estimated that only 45 Mariana fruit bats remain in Guam in a single roost site on Andersen Air Force Base.

A moth, *Anatrachyntis* sp. (Lepidoptera: Cosmopterigidae), is a probable pollinator of *C. micronesica* and possibly an obligate symbiont, i.e., it may not survive without the cycad. Larvae are numerous in male cones following pollen shedding, and they pupate in silken cocoons on the surfaces of cones (Marler and Muniappan, 2006). These authors hypothesized that the moth contributes to rapid degradation of the large and metabolically costly cone tissue after pollen dispersal. Terry et al. (2009) used sticky traps to sample insects and pollen in the vicinity of female *C. micronesica* cones. They observed that 30% of the pollen grains were associated with *Anatrachyntis* moths or moth scales and <5% with other insects; over 60% of the pollen was not associated with any insect, suggesting most of the pollen is dispersed by wind. Based on these observations, the authors hypothesized that *Anatrachyntis* sp. is an important pollinator of the tree.

Cycads are also economically valuable. The king sago palm is the most favored ornamental cycad species used in the international horticulture industry; nearly 110,000 plants were exported worldwide in 1993 (Whitelock, 2002). According to a report of the Convention on International Trade in Endangered Species, 99% of the 30 million cycads traded internationally from 1977 to 2001 originated from propagation nurseries (Anon., 2003a). Before 2003, 17 countries were involved in the international cycad trade (Anon., 2003b). Soon after the arrival of the cycad aulacaspis scale in Florida, exports of cycads from the state probably spread the scale internationally (Marler et al., 2021). All former cycad propagation nurseries in Florida have ceased production and export of the plants.

## THE ECOLOGY OF THE PROBLEM

The cycad aulacaspis scale is a member of the armored scale family Diaspididae. Only two other species of *Aulacaspis* occur in North America, both of which are considered agricultural pests. *Aulacaspis rosae* is a



**Figure 5.** *Cycas micronesica* adversely affected by the cycad aulacaspis scale, *Aulacaspis yasumatsui*, in Guam: (a) mature tree at Tarague; (b) dead mother tree with living pup at Tarague; (c) dying young plant at Star Cave; (d) infested leaf petioles and seeds of mature tree on the campus of the University of Guam, Mangilao. (a-d: R. D. Cave, University of Florida)

pest of roses (Dekle, 1976), and *Aulacaspis tubercularis* is a pest of mangoes (Hodges and Hamon, 2016). Both species are adventive in North America and have a circumtropical distribution. Outside Thailand, the cycad aulacaspis scale is a non-native insect, so it is not a keystone species or a unique prey or host for any native predator or parasitoid.

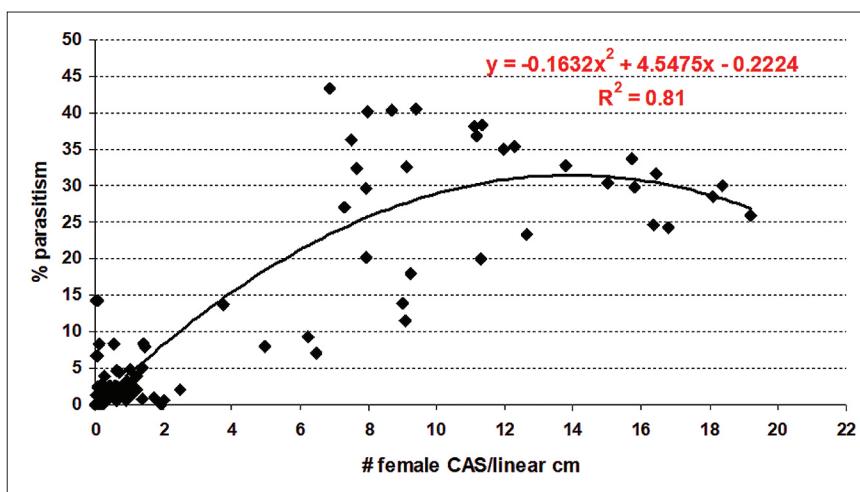
Damage from the cycad aulacaspis scale in Guam, Rota, Palau, and other Micronesian islands threatens the ancient, once-extensive native forests of *C. micronesica* with destruction. The armored scale weakens cycad trees, reducing their resistance to tropical cyclone winds and delaying recovery after a storm (Marler and Lawrence, 2013). Dead cycad trees are not being replaced because the scale kills seeds and seedlings (Marler and Cruz, 2019). Native animals that depend on *C. micronesica* as food are adversely affected by the loss of plants (Haynes and Marler, 2005).

Chemical pest management of the cycad aulacaspis scale is expensive because applications of horticultural oils or synthetic pesticides must be made at frequent, regularly scheduled intervals (Howard et al., 1999; Emshousen et al., 2004; Hara et al., 2005; Bográn et al., 2006). Pesticide treatments are not always effective because there are physical refuges on the plant where scales remain inaccessible to treatments. Moreover, broad-spectrum pesticides are highly toxic to the parasitoids and predators of the cycad aulacaspis scale (Smith and Cave, 2006a). Pesticide applications to the cycad forests of Guam and other western Pacific islands would be economically unfeasible and harmful to native wildlife.

## PROJECT HISTORY THROUGH AGENT ESTABLISHMENT

### Biological Control Efforts in Florida

Classical biological control of the cycad aulacaspis scale in Florida began in 1998 when the parasitic wasp *Coccobius fulvus* (Hymenoptera: Aphelinidae) and the predatory beetle *Cybocephalus nipponicus* (Coleoptera: Cybocephalidae) (erroneously identified as *C. binotatus* [Smith and Cave, 2006b]), both from Thailand, were imported, released, and established in Miami-Dade County (Hodges et al., 2003). About 15,000 individuals of *C. fulvus* were released during February–April 2002 in 13 Florida counties and broadened the distribution of the wasp throughout southern Florida (Hodges et al., 2003). *Coccobius fulvus* individuals subsequently collected from northern Vietnam were released in Gainesville, Florida in 2007, and this cold-hardy race



**Figure 6.** Rate of parasitism of female cycad aulacaspis scales (CAS), *Aulacaspis yasumatsui*, by *Coccobius fulvus* in relation to female scale density on *Cycas revoluta* in Florida. (R. D. Cave, University of Florida)

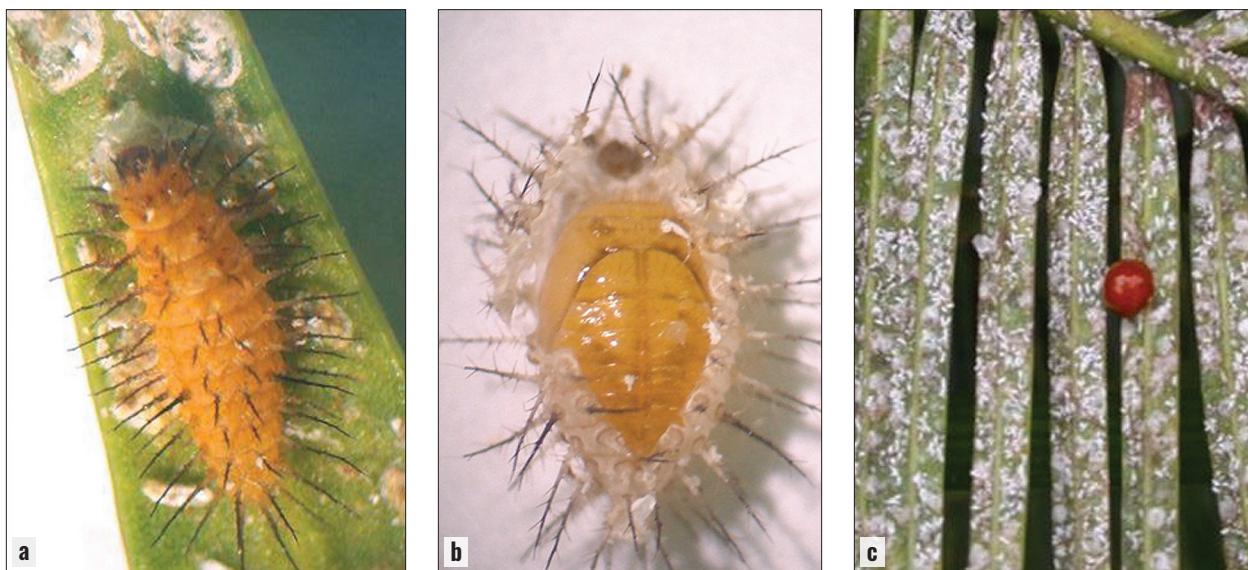
became established in northern Florida (R. Nguyen, pers. comm.). The wasp is now widespread throughout Florida, but its northern range is apparently defined by its intolerance of low winter temperatures. Rates of parasitism may be nearly 100% on individual leaflets, but overall parasitism by *C. fulvus* on a plant is usually between 10 and 40%, with greater parasitism occurring on leaves with high scale densities (Fig. 6). At extremely high densities, parasitism rates decrease because the scale population on a leaf is layered; scales on the plant surface are covered by other scales on top of scales, so are not accessible to female *C. fulvus*.

Larvae and adults of *C. nipponicus* are frequently observed in abundance on king sago palms infested with the cycad aulacaspis scale throughout Florida. The life history of the beetle was studied by Smith and Cave (2006b). Adults are long-lived and consume hundreds of scales during adulthood (Table 1). Females may lay over 300 eggs during their lifetime. The predator is widely distributed in Southeast Asia, where it occurs in very large numbers on scale-infested cycads in southern China and Vietnam (R. D. Cave, pers. obs.). *Cybocephalus nipponicus* was released in the northeastern United States to control euonymous scale (*Unaspis euonymi*), where it became established (Drea and Carlson, 1988; Alvarez and Van Driesche, 1998). According to label data on specimens in the Florida State Collection of Arthropods, *C. nipponicus* has been in Florida since at least 1990 (Smith and Cave, 2006c). The species also occurs in Texas and Hawaii. The wasp *Aphanogmus albicoxalis* (Hymenoptera: Ceraphronidae) parasitizes the prepupae and pupae of *C. nipponicus* (Evans et al., 2005). This parasitoid is native to Florida and may reduce the biological control capability of *C. nipponicus* there.

**Table 1.** Average longevity (days) and number of cycad aulacaspis scales (*Aulacaspis yasumatsui*) consumed per day and per life stage of *Cybocephalus nipponicus* (at 25°C [77°F], data from Smith and Cave, 2006), *Phaenochilus kashaya* (at 25°C, data from Manrique et al., 2012), and *Rhyzobius lophanthae* (at 24°C [75°F], data from Thorson, 2009). ND = no data.

Beetle Life Stage	<i>C. nipponicus</i>			<i>P. kashaya</i>			<i>R. lophanthae</i>		
	Longevity	Daily consumption	Total consumption	Longevity	Daily consumption	Total consumption	Longevity	Daily consumption	Total consumption
<b>Instars I–III</b>	ND	ND	ND	19	4–8	130	14	1–5	29
<b>Instar IV</b>	ND	ND	ND	12	21	246	6	5	58
<b>Larva (total)</b>	14	ND	ND	31	4–21	380	20	1–5	87
<b>Adult female</b>	110	4	440	158	29	915	104	3	281
<b>Adult male</b>	89	4	356	130	29	753	103	3	194

During exploration in Asia to find new natural enemies of the cycad aulacaspis scale, the lady beetle *Phaenochilus kashaya* (Coleoptera: Coccinellidae) (Fig. 7) was discovered in Thailand in 2007 (Cave et al., 2009a) and collected again in 2009. The beetle is not known to occur elsewhere (Giorgi and Vandenberg, 2012). Adults, larvae, and pupae were observed on *Cycas siamensis* in a forest near the Sakaerat Environmental Research Station in eastern Thailand. The cycads in the area had either very sparse infestations of the cycad aulacaspis scale or no scales at all (R. D. Cave, pers. obs.). The biology of this predator was studied in a quarantine facility by Manrique et al. (2012). Fourth instars eat about 3–5 times more scales/day than earlier instars at 25°C (77°F), and therefore consume more total scales than *C. nipponicus*. The consumption of scales by *P. kashaya* larvae is about 12 times more scales/day than by larvae of the predatory lady beetle *Rhyzobius lophanthae* (Table 1; Thorson, 2009). Adult females of *P. kashaya* can live up to six months at 25°C and lay eggs until shortly before death; males can live more than four months (Table 1). At 20°C (68°F), adult females and males live more than seven and five months, respectively. Because *P. kashaya* adults eat more scales per day and live considerably longer than *R. lophanthae* adults, *P. kashaya* can kill about 3.5 times more scales than *R. lophanthae* (Table 1). Female *P. kashaya* at 20°C each produce about



**Figure 7.** *Phaenochilus kashaya* larva, pupa, and adult. (a–c: R. D. Cave, University of Florida)

339 eggs during their adult life, while *R. lophantheae* adults feeding on cycad aulacaspis scales at 24°C (75°F) each lay only about 50 eggs (Thorson, 2009). Given these data, *P. kashaya* is undoubtedly a more voracious and prolific predator of cycad aulacaspis scales than *R. lophantheae* or *C. nipponicus*. A petition to release *P. kashaya* from quarantine in Florida was denied by USDA-APHIS-PPQ for multiple reasons. The natural enemy has not yet been released for biological control of the cycad aulacaspis scale anywhere.

The parasitoid *Arrhenophagus chionaspidis* (Hymenoptera: Encyrtidae) attacks cycad aulacaspis scales at rates ranging from 18 to 83% in China and Vietnam (R. D. Cave, unpublished data in report to APHIS PPQ). Material collected in Asia in 2007 was brought to quarantine in Florida for study and mass rearing. The parasitoid is very difficult to rear, and colonies of it could not be maintained. *Arrhenophagus chionaspidis* was discovered attacking cycad aulacaspis scale in Florida in 2012 (E. Rohrig, pers. comm.; R. D. Cave, pers. obs.). Ball and Stange (1979) reported the species attacking white peach scale (*Pseudaulacaspis pentagona*) in Florida. However, Bennett and Noyes (1989) subsequently stated that the *Arrhenophagus* species reported by Ball and Stange (1979) is *Arrhenophagus albitibiae*, a species described from Japan and known from Hong Kong and Sri Lanka. Therefore, it is uncertain if the *Arrhenophagus* species attacking cycad aulacaspis scale in Asia and Florida is *A. chionaspidis*, *A. albitibiae*, or an undescribed species. Molecular analysis might be able to resolve this conundrum. In Asia, the parasitoid was collected from plants with very heavy infestations of cycad aulacaspis scale. Therefore, *A. chionaspidis* does not appear to have potential as a biological control agent of cycad aulacaspis scale.

*Aprostocetus purpureus* (Hymenoptera: Eulophidae) was collected from female cycad aulacaspis scales in China and Vietnam in 2006 and brought to quarantine in Florida for study and mass rearing. The parasitoid was very difficult to rear, and colonies of it could not be maintained. This species has a wide distribution throughout India and Southeast Asia (Noyes, 2019). In Asia, it was collected from plants with very heavy infestations of cycad aulacaspis scale (R. D. Cave, pers. obs.). For these reasons, *A. purpureus* does not appear to have potential as a biological control agent of cycad aulacaspis scale.

Castillo et al. (2011) tested the entomopathogenic fungus *Cordyceps javanica* (given as *Isaria fumosorosea*) in the commercial product PFR97® (Certis USA, Columbia, MO) as a mortality agent of the cycad aulacaspis scale at 20°C and 30°C (86°F) in the laboratory. A concentration of  $5.4 \times 10^7$  blastospores per ml ( $1.8 \times 10^6/\text{fl oz}$ ) of water applied to 1<sup>st</sup> instars resulted in mean infection rates of 73% at 30°C and 84% at 20°C eight days after application. The LT<sub>50</sub> was lower at 30°C than at 20°C. These results indicate that *C.*

*javanica* may be a new biological control tool for suppressing infestations of cycads by the cycad aulacaspis scale, at least in horticultural settings.

## Biological Control Efforts in Hawaii

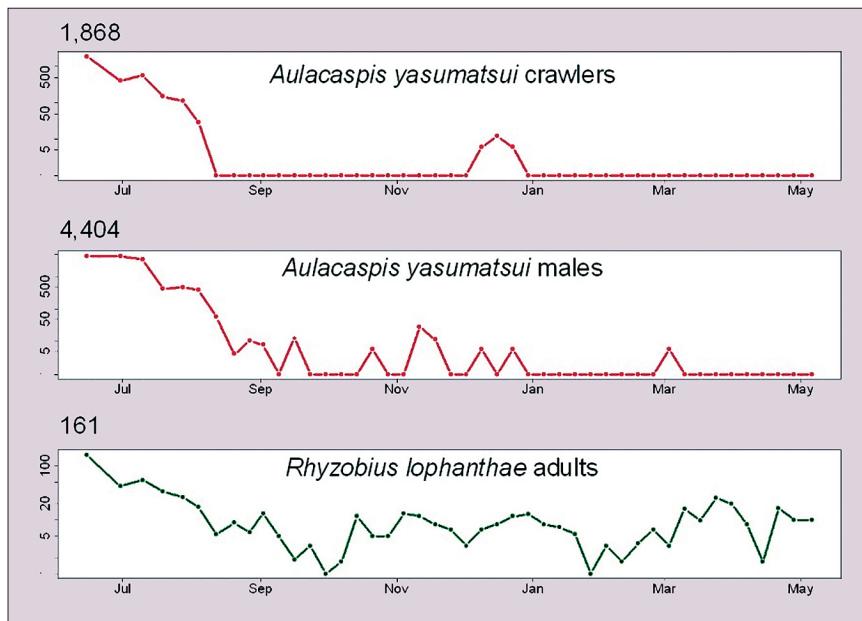
No program of classical biological control against the cycad aulacaspis scale has been implemented in Hawaii. However, some natural enemies previously introduced to Hawaii have expanded their prey or host ranges to attack the scale. *Rhyzobius lophantheae*, introduced into Hawaii in 1894 for the control of scale insects (Funasaki et al., 1988), readily began preying upon cycad aulacaspis scale in Hawaii when the pest first arrived. It is considered the most promising agent for scale management (Hara et al., 2005), and it can be effective under a range of conditions from dry to mesic habitats (M. G. Wright, pers. obs.).

The parasitoid *Aphytis lingnanensis* (Hymenoptera: Aphelinidae) was introduced into Hawaii in 1964 as a biological control agent for Florida red scale, *Chrysomphalus aonidum* (Davis and Krauss, 1964). *Aphytis lingnanensis*, or a cryptic species very similar to it (G. A. Evans, pers. comm. to B. R. Kumashiro, 2009), appears to have a significant effect on cycad aulacaspis scale populations in Hawaii. Plants with quite severe infestations seem to survive the impacts of the scale insect when the parasitoid is present and causes high levels of scale mortality (M. G. Wright, pers. obs.). *Aphytis lingnanensis*, or a cryptic species very similar to it, was initially discovered as a parasitoid of the cycad aulacaspis scale in southern Texas (Flores and Carlson, 2009), but its influence on scale populations there was not evaluated.

In 2008, Bernarr R. Kumashiro of the Hawaii Department of Agriculture reared two other parasitoids from cycad leaves infested with the cycad aulacaspis scale and assumed they had emerged from this host rather than another armored scale species undetected on the leaves (B. R. Kumashiro pers. comm. to G. A. Evans, 2008). Gregory A. Evans of the USDA Systematic Entomology Laboratory identified one of these parasitoids as “*Pteroptrix leptocera* Huang [Hymenoptera: Aphelinidae] or a species very similar to it and new” (G. A. Evans pers. comm. to B. R. Kumashiro, 2009). Species of *Pteroptrix* are known as parasitoids of armored scales (Chen and Li, 2017) and one soft scale and a whitefly (Herting, 1972), but the precise hosts of *P. leptocera* are not known. Interestingly, Hui Ren of the Guangdong Entomological Institute reared *Pteroptrix chinensis*, a generalist parasitoid of scale insects (references in Noyes, 2019), from cycad aulacaspis scales in China (Cave, 2005). Evans identified the second parasitoid as *Plagiomerus* sp. (Hymenoptera: Encyrtidae). Species of *Plagiomerus* are known to parasitize several species of armored scales; *Plagiomerus aulacaspis* parasitizes *Aulacaspis citri* (Tan and Zhao, 1998). *Pteroptrix leptocera* and *Plagiomerus* sp. are probably self-introductions in Hawaii. Little is known of the effect of different environments and cycad species on the effectiveness of *Aphytis* sp., *Pteroptrix* sp., or *Plagiomerus* sp. as biological control agents of cycad aulacaspis scale.

## Biological Control Efforts in Guam

In November 2004, about 100 adults of *R. lophantheae* were collected on Maui in Hawaii and imported to Guam (Moore et al., 2005b). This predatory beetle was chosen as the first biological control agent for introduction against the cycad aulacaspis scale in Guam because it was effective in Hawaii and relatively easy to introduce from there. Beetles were reared on scale-infested leaves cut from *C. micronesica*, collected from the laboratory rearing colony, and released in Guam National Wildlife Refuge at Ritidian Point starting in February 2005. Populations of the predator established readily. By July 2005, high densities of adults were observed on cycads at Urunao Beach, 1 km (0.6 mi) from Ritidian Point where one observer counted 57 beetles in one minute on scale-infested cycad leaves. Establishment and dispersion of *R. lophantheae* were monitored using yellow sticky traps between July 2005 and May 2006 (Fig. 8). Following establishment of *R. lophantheae* at Ritidian Point, 7,454 laboratory-reared and field-collected beetles were released on scale-infested cycads at 115 sites throughout Guam.



**Figure 8.** Insects trapped on yellow sticky cards at Ritidian Point, Guam following field release of *Rhyzobius lophantheae* in February 2005. X-axis runs from July 2005 through May 2006; Y-axis, in log scale, is the number of insects trapped per square meter per day. (from Moore et al., 2005b, reprinted with permission)

By 2010, *R. lophantheae* larvae or adults could be found on almost every infested cycad plant on Guam, and their predation on scales allowed mature cycads to survive. However, the *C. micronesica* population is not recovering because almost all seeds and seedlings are still being killed by the cycad aulacaspis scale and other causes (Marler and Terry, 2011). Marler et al. (2013) showed that predation rates by *R. lophantheae* are significantly lower on scales feeding close to the ground, and they suggested that this may partially account for the inability of the beetle to protect seedling plants. Although the causes of reduced scale predation near the ground are unknown, the authors suggested that a parasitoid might not have the same limitations because it would be much smaller than *R. lophantheae* and better able to reach scales within the cracks and crevices on *C. micronesica* and *C. revoluta* stems and roots. Unfortunately, no known parasitoid of the cycad aulacaspis scale attacks the scales settled on the coralloid roots in the soil.

In August 2005, R. Muniappan imported to Guam some 500 adults of the parasitoid *C. fulvus* that were sourced from a laboratory colony in Florida that had been established with parasitoids from China (Moore et al., 2005b). Of this shipment, 250 parasitoids were released in a cage with a potted scale-infested *C. revoluta* plant, and the other 250 parasitoids were released on scale-infested *C. micronesica* plants in the field at Marbo Cave on the northeastern coast of the island. This site was selected because *R. lophantheae* was not in the Marbo Cave area at that time because it had not been released there and had not yet dispersed into that area. Another 250 parasitoids received in September 2005 were released at the Marbo Cave site, as attempts to culture this species in the quarantine laboratory were not progressing satisfactorily. To determine if the parasitoid had established, a scale-infested frond of *C. micronesica* from the Marbo Cave area was collected four weeks after the release for examination under a binocular microscope. One parasitoid exit hole was observed on this frond. Four parasitoid exit holes were found when the same procedure was repeated in October 2005, but no exit holes were found on a sample examined in November 2005.

In a second attempt to introduce *C. fulvus*, G. V. P. Reddy imported adults from a laboratory colony in Florida, which had been established from wasps collected in Thailand. Some of these wasps were released on scale-infested cycads in Talofofo, Guam in 2008 (G. Reddy, pers. comm.). Attempts to establish a laboratory colony failed, and there was no evidence of establishment in the field.

In a third attempt to introduce *C. fulvus*, A. Moore imported specimens collected in Florida in September 2014 and October 2014. Half of both shipments were released at Ritidian Point, Guam. Attempts to establish a laboratory colony failed, and there was no evidence of establishment in the field. The reasons why establishment failed after the 2008 and 2014 releases are unknown. Possibilities are that too few individuals were released, parasitized scales were preyed on by *R. lophantheae*, and/or the individuals released were not sufficiently vigorous to find hosts.

In 2012, about 100 *A. lingnanensis* adults from Honolulu, Hawaii, were imported. These wasps were reared by University of Hawaii entomologist Leyla Kaufman from cycad aulacaspis scales infesting *C. revoluta* in a home garden. Upon arrival in Guam, the wasps were placed in a cage containing scale-infested *C. micronesica* leaves. All visible *R. lophantheae* adults and larvae were removed from these leaves, but there were undetected beetle eggs and 1<sup>st</sup> instars beneath scale covers to repopulate the leaves and eat all the scales before any adult wasps emerged. Thus, a laboratory colony was not established, and no field releases were made.

G. V. P. Reddy imported *A. chionaspidis* from a laboratory colony in Florida. Field releases in Guam were made during 2008. However, this parasitoid was already present in Guam via accidental self-introduction (G. V. P. Reddy, pers. comm., 2022). High proportions of the cycad aulacaspis scales at Ritidian Point were observed to be parasitized by *A. chionaspidis* in February 2013 (A. Moore, pers. obs.). The species identification was confirmed by John Noyes (Natural History Museum, London, UK). Surveys during 2017 and 2018 indicated that *A. chionaspidis* is the only parasitoid of cycad aulacaspis scale in Guam.

## HOW WELL DID BIOLOGICAL CONTROL WORK?

Despite releases of *C. fulvus* parasitoids and *C. nipponicus* predators when the cycad aulacaspis scale was restricted to southeastern Florida, the scale quickly spread due to the movement of infested plants or natural dispersal by the wind. Although the natural enemies also dispersed throughout Florida, they did not provide adequate control (Wiese et al., 2005; Cave, 2006). Rates of parasitism by *C. fulvus* did not exceed 50% on leaves (Fig. 6), so parasitism was inadequate for effective control of the scale due to its rapid development and high fecundity (Cave et al., 2009b; Ravuiwasa et al., 2012). Although adults of *C. nipponicus* consume about four scales per day (Smith and Cave, 2006b) and the larvae are also predaceous, plants with the predator present were still heavily infested by the scale in Florida and Asia. No data have been collected to quantify the effect of *A. chionaspidis* on scale populations in Florida.

Because biological control of the cycad aulacaspis scale has been ineffective in Florida, nurseries in the state no longer grow king sago palms for retail businesses or export to out-of-state markets. Also, very few ornamental king sago palms remain in Florida's urban landscape; those that remain are infested by cycad aulacaspis scale, but they survive due to chemical applications by landscape managers and homeowners.

The introduction of *R. lophantheae* in Guam appears to have had a significant suppressive effect on cycad aulacaspis scale populations on large trees. Larvae and adults of the predator are found on almost every scale-infested cycad in Guam, preventing the scale from killing mature cycads. Recent observations of several trees revealed the presence of *R. lophantheae* and almost 100% predation of scales on leaves. Predation rates in the tree crowns and under bracts have not been measured. Some trees in isolated areas have dense cycad aulacaspis scale infestations on their leaves, megasporophylls, and seeds, and there is no indication of predation at these sites. Although intense predation occurs on mature trees, overall plant health often looks poor, and very few trees are producing seeds. Unfortunately, the *C. micronesica* population is not recovering because almost all seeds and seedlings are being killed by the scale. Predation by *R. lophantheae* does not protect either seeds or seedlings. Marler et al. (2013) showed that predation by *R. lophantheae* is significantly reduced close to the ground and suggested that this may partially account for the failure of the beetle to protect seedlings.

Parasitism by *A. chionaspidis* occurs across Guam. Some trees have high rates of parasitism, but others have no evidence of parasitism. Where the parasitoid is present, infested plants still have populations of female scales that are producing eggs. Attempts to introduce the parasitoids *C. fulvus* and *A. lingnanensis* were not successful.

## BENEFITS OF BIOLOGICAL CONTROL OF CYCAD AULACASPI SCALE

There probably is no hope of rebuilding the cycad production industry in Florida. No natural enemies of cycad aulacaspis scale have shown an ability to reduce scale populations to levels that can be practically and economically managed with chemical control. No biological control agents suppress the pest adequately.

Successful biological control of the cycad aulacaspis scale in the urban landscape, be it in Florida, Texas, Hawaii, or elsewhere, would benefit the environment where ornamental cycads have survived. Broad-spectrum pesticides applied as a soil drench and as foliar sprays, and horticultural oils applied to the leaves, are the primary means used by the landscape care industry and homeowners to protect cycads. However, chemical control can be expensive. For example, dinotefuran is a water-soluble systemic pesticide that can be applied either as a drench or twice a year to foliage for temporary control (Caldwell, 2005). A 1.4-kg (3-lb) container of Safari 20SG Systemic Insecticide with Dinotefuran costs about \$422–468 ([www.amazon.com](http://www.amazon.com); [www.domyownpestcontrol.com](http://www.domyownpestcontrol.com)). It is therefore not economical for homeowners to use it to treat just a few plants. On the other hand, applications of horticultural oils must be made at frequent, regular intervals (Howard et al., 1999; Emshousen et al., 2004; Hara et al., 2005; Bográn et al., 2006), and therefore their use is also costly. Some homeowners have applied pesticides not registered for use on cycads, such as flea and tick sprays (R. D. Cave, pers. obs.). If biological control agents cannot effectively control the cycad aulacaspis scale, then landscapers, homeowners, and botanical garden managers will continue to use costly pesticides that interfere with the resident natural enemies and contaminate soil and water.

Mature *C. micronesica* trees in Guam's forests are still succumbing to infestations by the cycad aulacaspis scale and are not being replaced by young plants. It is obvious that without a change, this endemic plant, the most abundant tree in Guam's forests only two decades ago, is headed towards local extinction. Restoration of Guam's forests to their pristine state is not possible with our current understanding of the scale's natural enemies. However, there is an urgent need to control cycad aulacaspis scale so that some cycad recovery can take place, without further loss of biodiversity.

Field release of the lady beetle *P. kashaya*, a voracious, oligophagous predator of armored scales, could contribute significantly to the biological control of the cycad aulacaspis scale in Guam and other western Pacific islands. Both the larval and adult stages consume the cycad aulacaspis scale, and the insect is easily reared in the laboratory. There is evidence in its homeland (Thailand) that it can suppress cycad aulacaspis scale populations to very low levels. If released in Guam, Rota, Tinian, and Palau, this beetle would likely reduce the abundance of cycad aulacaspis scale to levels that no longer threaten the survival of native *C. micronesica* forests on those islands. The actions of other natural enemies, such as *R. lophantheae* and *A. chionaspidis*, might also be enhanced. Although Agriculture and Agri-Food Canada, in its review of a petition to release *P. kashaya*, did not recommend release in the southeastern United States, the agency did recommend that *P. kashaya* be approved for release in Guam (P. G. Mason in litt. to R. Tichenor, 2014). However, USDA-APHIS-PPQ did not make any judgment on the latter recommendation. Currently, there are no plans to release *P. kashaya* in Guam because Guam lacks the professional capacity and funding to develop and implement a biological control program. However, an initiative to remedy this situation is underway. On the other hand, competition between *P. kashaya* and resident natural enemies (*R. lophantheae*, other lady beetles, and *A. chionaspidis*) in Guam must be considered.

New attempts to establish *C. fulvus* in Guam might lead to better biological control of the cycad aulacaspis scale, but studies are needed to investigate its searching behavior and ecology in the environment. Species of *Aphytis* that have been reared from cycad aulacaspis scales collected in China, Texas, and Hawaii need to be carefully examined taxonomically and biologically to determine their potential as biological control agents in Florida and Guam. Introduction of *C. nipponicus* may offer hope to save the native forests of *C. micronesica* in Micronesia.

## REFERENCES

- Alvarez, J. M. and R. Van Driesche. 1998. Biology of *Cybocephalus* sp. nr. *nipponicus* (Coleoptera: Cybocephalidae), a natural enemy of euonymus scale (Homoptera: Diaspididae). *Environmental Entomology* 27: 130–136.
- Anon. 2003a. Review of significant trade cycads. PC14 Doc. 9.2.2. Plants Committee, Convention on International Trade in Endangered Species of Wild Fauna and Flora. [cites.org/sites/default/files/eng/com/pc/14/E-PC14-09-02-02-A1.pdf](https://cites.org/sites/default/files/eng/com/pc/14/E-PC14-09-02-02-A1.pdf)
- Anon. 2003b. CITES significant trade review of cycads. PC13 Doc. 12.2.2. Plants Committee, Convention on International Trade in Endangered Species of Wild Fauna and Flora. [cites.org/sites/default/files/eng/com/pc/13/E-PC13-12-02-02.pdf](https://cites.org/sites/default/files/eng/com/pc/13/E-PC13-12-02-02.pdf)
- Ball, J. C. and L. A. Stange. 1979. Report of *Arrhenophagus chionaspidis* on *Pseudaulacaspis pentagona* in Florida. *Florida Entomologist* 62(4): 414.
- Bennett, F. D. and J. S. Noyes. 1989. Three chalcidoid parasites of diaspines and whiteflies occurring in Florida and the Caribbean. *Florida Entomologist* 72(2): 370–373.
- Bográn, C. E., B. A. Castro, and S. Ludwig. 2006. The cycad aulacaspis scale, a pest of sago palms in Texas. University of Texas Cooperative Extension Publication EEE-00038.
- Caldwell, D. 2005. Observations on some insect pests of woody ornamentals: black olive caterpillar, Geiger tree tortoise beetle and cycad aulacaspis scale in Naples, Florida. *Proceedings of the Florida State Horticultural Society* 118: 322–325.
- Calonje, M. 2008. Guam and Rota 2007: working against cycad extinction. *Montgomery Botanical News* 16(1): 1, 3.
- Castillo, J. A., P. B. Avery, R. D. Cave, and C. O. Montemayor. 2011. Mortality of the cycad aulacaspis scale (Hemiptera: Diaspididae) by the entomopathogenic fungus *Isaria fumosorosea* Wize under laboratory conditions. *Journal of Entomological Science* 46(3): 256–264.
- Cave, R. D. 2005. Biological control of *Aulacaspis yasumatsui*. *The Cycad Newsletter* 28(5): 8–9.
- Cave, R. D. 2006. Biological control agents of the cycad aulacaspis scale, *Aulacaspis yasumatsui*. *Proceedings of the Florida State Horticultural Society* 119: 422–424.
- Cave, R. D., R. Nguyen, V. Manrique, and P. B. Avery. 2009a. New research on two natural enemies of the cycad aulacaspis scale. *The Cycad Newsletter* 32(2/3): 22–23.
- Cave, R. D., C. Sciacchettano, and R. Diaz. 2009b. Temperature-dependent development of the cycad aulacaspis scale, *Aulacaspis yasumatsui* (Hemiptera: Diaspididae). *Florida Entomologist* 92: 578–581.
- Chen, Y. and C.-D. Li. 2017. A new species, first report of a male and new distributional records for three species of *Pteroptyx* (Hymenoptera: Aphelinidae) from China. *Biodiversity Data Journal* 5: e12387.
- Davis, C. J. and N. L. H. Krauss. 1964. Recent introductions for biological control in Hawaii - IX. *Proceedings of the Hawaiian Entomological Society* 18: 391–398.
- Dekle, G. W. 1976. *Arthropods of Florida and Neighboring Land Areas, Volume 3 (revised)*. Contribution No. 60 Entomology Section, Florida Department of Agriculture and Consumer Services, Gainesville, Florida, USA.
- Dimkpa, S. O. N., R. E. Baraka, M. D. Tobin-West, and E. Okwukwu. 2021. Cycad aulacaspis scale (CAS) *Aulacaspis yasumatsui* Takagi as a major pest of sago palm *Cycas* spp. in Nigeria. *International Journal of Entomology and Nematology Research* 5(1): 1–10.
- Donnegan, J. A., S. L. Butler, W. Grabowiecki, B. A. Hiserote, and D. Limtiaco. 2004. Guam's forest resources, 2002. USDA Forest Service, Pacific Northwest Research Station, Portland Oregon, USA. [www.fs.fed.us/pnw/pubs/pnw\\_rb243.pdf](http://www.fs.fed.us/pnw/pubs/pnw_rb243.pdf)
- Drea, J. J. and R. M. Carlson. 1988. Establishment of *Cybocephalus* sp. (Coleoptera: Nitidulidae) from Korea on *Unaspis euonymi* (Homoptera: Diaspididae) in the eastern United States. *Proceedings of the Entomological Society of Washington* 90: 307–309.
- Emshousen, C., C. Mannion, and H. Glenn. 2004. Management of cycad aulacaspis scale, *Aulacaspis yasumatsui* Takagi. *Proceedings of the Florida Horticultural Society* 117: 305–307.
- Evans, G. A., P. Dessart, and H. Glenn. 2005. Two new species of *Aphanogmus* (Hymenoptera: Ceraphronidae) of economic importance reared from *Cybocephalus nipponicus* (Coleoptera: Cybocephalidae). *Zootaxa* 1018: 47–54.
- Flores, D. and J. Carlson. 2009. Fortuitous establishment of *Rhyzobius lophanthae* (Coleoptera: Coccinellidae) and *Aphytis lingnanensis* [sic] (Hymenoptera: Encyrtidae) in South Texas on the cycad aulacaspis scale, *Aulacaspis yasumatsui* (Hemiptera: Diaspididae). *Southwestern Entomologist* 34(4): 489–492.
- Funasaki, G.Y., P.-Y. Lai, L. M. Nakahara, J. W. Beardsley, and A. K. Ota. 1988. A review of biological control introductions in Hawaii: 1890 to 1985. *Proceedings of the Hawaiian Entomological Society* 28: 105–160.

- Germain, J. F. and G. S. Hodges. 2007. First report of *Aulacaspis yasumatsui* (Hemiptera: Diaspididae) in Africa (Ivory Coast), and update on distribution. *Florida Entomologist* 90: 755–756.
- Giorgi, J. A. and N. J. Vandenberg. 2012. Review of the lady beetle genus *Phaenochilus* Weise (Coleoptera: Coccinellidae: Chilocorini) with description of a new species from Thailand that preys on cycad aulacaspis scale, *Aulacaspis yasumatsui* Takagi (Hemiptera: Sternorrhyncha: Diaspididae). *Zootaxa* 3478: 239–255.
- Hara, A., R. Y. Niino-DuPonte, C. M. Jacobson, S. Chun, T. McDonald, W. T. Nagamine, and R. A. Heu. 2005. Cycad scale on sago palm. University of Hawai'i at Mānoa, Hawaii. (Insect Pests; IP-23).
- Haynes, J. and T. E. Marler. 2005. Exotic invasive pest insect critically threatening Guam's vulnerable flora, fauna and island ecosystem. Montgomery Botanical Garden, Miami, FL. [www.montgomerybotanical.org/media/CAS/Haynes-Marler-Guam-CAS-Overview.pdf](http://www.montgomerybotanical.org/media/CAS/Haynes-Marler-Guam-CAS-Overview.pdf)
- Herting, B. 1972. *Homoptera. A Catalogue of Parasites and Predators of Terrestrial Arthropods. Vol. 2. Section A. Host or Prey/Enemy*. Commonwealth Agricultural Bureaux, Slough, U.K.
- Heu, R., M. Chun, and W. Nagamine. 2003. Sago palm scale, *Aulacaspis yasumatsui* Takagi (Homoptera: Diaspididae). State of Hawaii Department of Agriculture New Pest Advisory 99-01. [hdoa.hawaii.gov/pi/files/2013/01/npa99-01-spalmscale2.pdf](http://hdoa.hawaii.gov/pi/files/2013/01/npa99-01-spalmscale2.pdf)
- Hodges, G. and A. Hamon. 2016. White mango scale *Aulacaspis tubercularis* Newstead (Coccoidea: Diapidae). Pest Alert FDACS-P-01697, Florida Department of Agriculture and Consumer Services, Gainesville, Florida, USA.
- Hodges, G., F. G. Howard, and E. A. Buss. 2003. Update on management methods for cycad aulacaspis scale. Florida Cooperative Extension publication #ENY-680. [citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.526.4055&rep=rep1&type=pdf](http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.526.4055&rep=rep1&type=pdf)
- Hodgson, C. and J. H. Martin. 2001. Three noteworthy scale insects (Hemiptera: Coccoidea) from Hong Kong and Singapore, including *Cribropulvinaria tailungensis*, new genus and species (Coccidae), and the status of the cycad-feeding *Aulacaspis yasumatsui* (Diaspididae). *Raffles Bulletin of Zoology* 49: 227–250.
- Howard, F. W., A. Hamon, M. McLaughlin, T. Weissling, and S.-L. Yang. 1999. *Aulacaspis yasumatsui* (Homoptera: Sternorrhyncha: Diaspididae), a scale insect pest of cycads recently introduced into Florida. *Florida Entomologist* 82: 14–27.
- Macharia, I., P. Kibwage, H. M. Heya, F. Makathima, D. Olubayo, M. Guantai, W. Kinuthia, D. Ouvrard, and G. W. Watson. 2021. New records of scale insects and mealybugs (Hemiptera: Coccomorpha) in Kenya. *EPPO Bulletin* 51(3): 639–647.
- Manrique, V., D. A. Mancero-Castillo, R. D. Cave, and R. Nguyen. 2012. Effect of temperature on the development and consumption of *Phaenochilus kashaya* (Coleoptera: Coccinellidae), a predator of the cycad aulacaspis scale, *Aulacaspis yasumatsui*. *Biocontrol Science and Technology* 22(11): 1245–1253.
- Marler, T. E. 2012. Cycad aulacaspis scale invades the Mariana Islands. In: Stevenson, D. W., R. Osborne, and A. S. Taylor Blake (eds.). Proceedings of Cycad 2008. The 8<sup>th</sup> International Conference on Cycad Biology, Panama City, Panama, 13–15 January 2008. *Memoirs of the New York Botanical Garden* 106: 20–35.
- Marler, T. E. 2013. Increased threat of island endemic tree's extirpation via invasion-induced decline of intrinsic resistance to recurring tropical cyclones. *Communicative & Integrative Biology* 6(1): e223611.
- Marler, T. E. and G. N. Cruz. 2019. Source and sink relations mediate depletion of intrinsic cycad seed carbohydrates by *Aulacaspis yasumatsui* infestation. *HortScience* 54(10): 1712–1717.
- Marler, T. E. and M. V. Krishnapillai. 2020. Longitude, forest fragmentation, and plant size influence *Cycas micronesica* mortality following island insect invasions. *Diversity* 12: 194. <https://doi.org/10.3390/d12050194>
- Marler, T. and J. H. Lawrence. 2012. Demography of *Cycas micronesica* on Guam following introduction of the armoured scale *Aulacaspis yasumatsui*. *Journal of Tropical Ecology* 28: 233–242.
- Marler, T. E. and J. H. Lawrence. 2013. Phytophagous insects reduce cycad resistance to tropical cyclone winds and impair storm recovery. *HortScience* 48(10): 1224–1226.
- Marler, T. E., J. H. Lawrence, and G. Cruz. 2016. Topographic relief, wind direction, and conservation management decisions influence *Cycas micronesica* K.D. Hill population damage during tropical cyclone. *Journal of Geography and Natural Disasters* 6(3): 1000178.
- Marler, T. E., A. J. Lindström, and G. W. Watson. 2021. *Aulacaspis yasumatsui* delivers a blow to international cycad horticulture. *Horticulturae* 7: 147.
- Marler, T. E., R. Miller, and A. Moore. 2013. Vertical stratification of predation on *Aulacaspis yasumatsui* infesting *Cycas micronesica* seedlings. *HortScience* 48(1): 60–62.
- Marler, T. E. and A. Moore. 2010. Cryptic scale infestations on *Cycas revoluta* facilitate scale invasions. *HortScience* 45: 837–839.

- Marler, T. E. and R. Muniappan. 2006. Pests of *Cycas micronesica* leaf, stem, and male reproductive tissues with notes on current threat status. *Micronesica* 39(1): 1–9.
- Marler, T. E. and I. Terry. 2011. Arthropod invasion disrupts *Cycas micronesica* seedling recruitment. *Communicative & Integrative Biology* 4: 778–780.
- Marler, T. E. and L. I. Terry. 2021. *Aulacaspis yasumatsui* invasion reduced *Cycas micronesica* microstrobilus size and pollinator brood site competence. *Insects* 12: 1023.
- Moore, A., I. Iriarta, and R. Quintugua. 2005a. Asian cycad scale *Aulacaspis yasumatsui* Takagi (Homoptera: Diaspididae). Pest Sheet 2005-01. Cooperative Extension Service, Agricultural and Natural Resources Division, University of Guam, Mangilao, Guam.
- Moore, A., T. Marler, R. H. Miller, and R. Muniappan. 2005b. Biological control of cycad aulacaspis scale on Guam. *The Cycad Newsletter* 28: 6–8.
- Muniappan, R., G. W. Watson, G. A. Evans, A. Rauf, and N. von Ellenrieder. 2012. Cycad aulacaspis scale, a newly introduced insect pest in Indonesia. *HAYATI Journal of Biosciences* 19(3): 110–114.
- Normark, B. B., R. D. Normark, A. Vovides, L. Solís-Montero, R. González-Gómez, M. T. Pulido-Silva, M. A. Escobar-Castellanos, M. Dominguez, M. A. Perez-Farrera, M. Janda, and A. Cibrian-Jaramillo. 2017. Cycad aulacaspis scale (*Aulacaspis yasumatsui* Takagi, 1977) in Mexico and Guatemala: a threat to native cycads. *BioInvasions Records* 6(3): 187–193. <https://doi.org/10.3391/bir.2017.6.3.02>
- Noyes, J. S. 2019. Universal Chalcidoidea Database. WWW electronic publication. <https://www.nhm.ac.uk/our-science/data/chalcidoids/database/>
- Orapa, W. and R. D. Cave. 2010. Coccinellids for combating cycad scale: promising news from Palau and the USA. *Biocontrol News & Information* 31(1): 2N–3N.
- Ravuiwasa, K. T., C.-W. Tan, I. Bezirganoglu, and S.-Y. Hwang. 2012. Temperature-dependent demography of *Aulacaspis yasumatsui* (Hemiptera: Diaspididae). *Journal of Economic Entomology* 105(5): 1581–1590.
- Segarra-Carmona, A. and W. Pérez-Padilla. 2007. The cycad scale, *Aulacaspis yasumatsui* Takagi (Homoptera: Diaspididae): a new invasive pest to Puerto Rico. *Journal of Agriculture University of Puerto Rico* 92: 123–129.
- Smith, T. R. and R. D. Cave. 2006a. Pesticide susceptibility of *Cybocephalus nipponicus* and *Rhyzobius lophanthae* (Coleoptera: Cybocephalidae, Coccinellidae). *Florida Entomologist* 89(4): 502–507.
- Smith, T. R. and R. D. Cave. 2006b. Life history of *Cybocephalus nipponicus* Endrödy-Younga (Coleoptera: Cybocephalidae), a predator of *Aulacaspis yasumatsui* Takagi (Hemiptera: Diaspididae). *Proceedings of the Entomological Society of Washington* 108(4): 905–916.
- Smith, T. R. and R. D. Cave. 2006c. The Cybocephalidae (Coleoptera) of America north of Mexico. *Annals of the Entomological Society of America* 99(5): 776–792.
- Takagi, S. 1977. Appendix: a new species of *Aulacaspis* associated with a cycad in Thailand (Homoptera: Coccoidea). In: Nakao, S., S. Takagi, T. Tachikawa, and T. Wongsiri (eds.). Scale Insects Collected on Citrus and other Plants and Their Hymenopterous Parasites in Thailand. *Insecta Matsumurana New Series* 11: 61–72.
- Tan, Y. G. and J. Z. Zhao. 1998. Two new species of the genus *Plagiomerus* (Hymenoptera: Encyrtidae). *Acta Zootaxonomica Sinica* 23(2): 209–211. [in Chinese]
- Tang, W., J. Donaldson, J. Haynes, and I. Terry. 2006. Report and recommendations on cycad aulacaspis scale, *Aulacaspis yasumatsui* Takagi (Hemiptera: Diaspididae). IUCN/SSC Cycad Specialist Group - Subgroup on Invasive Species. [entnemdept.ufl.edu/pestalert/Cycad\\_Aulacaspis\\_Scale\\_report.pdf](http://entnemdept.ufl.edu/pestalert/Cycad_Aulacaspis_Scale_report.pdf)
- Terry, I. and T. Marler. 2005. Paradise lost? Tipping the scales against Guam's *Cycas micronesica*. *The Cycad Newsletter* 28: 21–23.
- Terry, I., M. Roe, W. Tang, and T. E. Marler. 2009. Cone insects and putative pollen vectors of the endangered cycad, *Cycas micronesica*. *Micronesica* 41(1): 83–99.
- Thorson, G. 2009. Evaluation of *Rhyzobius lophanthae* (Blaisdell) and *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae) as predators of *Aulacaspis yasumatsui* Takagi (Hemiptera: Diaspididae). MSc thesis, University of Florida, Gainesville, Florida, USA.
- Weissling, T. J., F. W. Howard, and A. B. Hamon. 1999. Cycad aulacaspis scale, *Aulacaspis yasumatsui* Takagi (Insecta: Homoptera: Sternorrhyncha: Diaspididae). University of Florida Extension publication #EENY-096. [edis.ifas.ufl.edu/IN253](http://edis.ifas.ufl.edu/IN253)
- Whitelock, L. M. 2002. *The Cycads*. Timber Press, Inc., Portland, Oregon, USA.
- Wiese, C., D. Amalin, R. Coe, and C. Mannion. 2005. Effects of the parasitic wasp, *Coccobius fulvus*, on cycad aulacaspis scale, *Aulacaspis yasumatsui*, at Montgomery Botanical Center, Miami, Florida. *Proceedings of the Florida State Horticultural Society* 118: 319–321.