

Ecology and Evolution of Cycad-Feeding Lepidoptera

Melissa RL Whitaker^{1,2} and Shayla Salzman^{2,3}

¹ Entomological Collection, Department of Environmental Systems Science, ETH Zürich, Weinbergstrasse 56/58, 8092 Zürich, Switzerland. mrl.whitaker@gmail.com.

² Museum of Comparative Zoology, Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA

³ School of Integrative Plant Science, Cornell University, 502 Mann Library, Ithaca, NY 14853, USA. sms728@cornell.edu.

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Correspondence: Dr. Melissa Whitaker; address: ETH Zürich, Schmelzbergstrasse 9, 8006 Zürich, Switzerland; phone: +41 774932944; email: mrl.whitaker@gmail.com

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Abstract: Cycads are an ancient group of tropical gymnosperms that are toxic to most animals—including humans—though the larvae of many moths and butterflies (order: Lepidoptera) feed on cycads with apparent immunity. These insects belong to distinct lineages with varying degrees of specialization and diverse feeding ecologies, presenting numerous opportunities for comparative studies of chemically-mediated eco-evolutionary dynamics. This review presents an evolutionary evaluation of cycad-feeding among Lepidoptera along with a comprehensive review of their ecology. Our analysis suggests that multiple lineages have independently colonized cycads from angiosperm hosts, yet only a few clades appear to have radiated following their transitions to cycads. Defensive traits are likely important for diversification, as many cycad specialists are warningly colored and sequester cycad toxins. The butterfly family Lycaenidae appears to be particularly predisposed to cycad-feeding and although aposematism is otherwise rare in this family, several cycad-feeding lycaenids are warningly colored and chemically defended. Cycad-herbivore interactions provide a promising but underutilized study system for investigating plant-insect coevolution, convergent and divergent adaptations, and the multi-trophic significance of defensive traits, therefore the review ends by suggesting specific research gaps that would be fruitfully addressed in Lepidoptera and other cycad-feeding insects.

1 Introduction

2 Lepidoptera (butterflies and moths) have long been used to test theories about the evolutionary
3 origins and consequences of ecological traits, and their larval associations with host plants have
4 served as a scientific cornerstone of research into coevolution and chemical ecology. An extensive
5 literature on the physiological, morphological, behavioral, genetic, and ecological mechanisms of
6 plant-butterfly interactions has developed over the last half century, largely in response to Ehrlich's &
7 Raven's seminal 1964 paper describing macroevolutionary patterns of host use among butterflies [1].
8 These studies have elucidated the biological basis and ecological significance of acquired chemical
9 defense in insects [2], identified key innovations underlying specialization [3], and described chemical
10 communication among plants, herbivores, and higher trophic levels [4, 5]. They have identified
11 phytochemical convergence among distantly related plant families [6] and documented molecular and
12 behavioral convergence among insects in their counteradaptations to plant defenses [7, 8]. Much of
13 the progress in this field has been borne from studies of agricultural systems and model interactions,
14 such as monarch butterflies specialized on latex- and cardenolide-producing milkweeds [6, 9, 10],
15 *Zygaena* moths that sequester and synthesize cyanogenic glucosides [11, 12], arctiid moths and their
16 pyrrolizidine alkaloid producing hostplants [13, 14], caterpillars specialized on plants defended by
17 furanocoumarins [15, 16], and pierid larvae feeding on glucosinolate-rich plants in the Brassicales
18 [17, 18]. These systems and others have taught us a great deal about how phytochemicals shape
19 plant-insect interactions over ecological and evolutionary timescales.

20 But for all its richness and impact, the literature on chemically-mediated plant-herbivore
21 interactions has a 'precariously narrow base' [19]: the overwhelming majority of research is focused
22 on insects that feed on a handful of angiosperm families, with comparatively little investigation into
23 non-angiospermous diets (but see [20–24]). To achieve a more comprehensive understanding of the
24 generalities and idiosyncrasies underlying plant-insect interactions, research needs to encompass a
25 broader selection of the rich taxonomic and chemical diversity of plants and their herbivores. To this
26 end, we present a fascinating study system comprised of cycads and their lepidopteran herbivores,
27 which we believe holds great promise for advancing long-standing and new hypotheses in ecology
28 and evolution.

29 Cycads (order: Cycadales) are a basal, pantropical group of dioecious gymnosperms with a fossil
30 record extending back over 265 million years [25]. With 75% of the 355 cycad species threatened with
31 extinction, they are the most imperiled plant order in the world [26–28]. Cycads possess an arsenal of
32 distinctive chemical defenses that are themselves deserving of review, and yet a number of insects use
33 cycads as larval and adult food plants. The majority of cycad-feeding (cycadivorous) insects belong to
34 a handful of lepidopteran families that exhibit varying degrees of host specialization and belong to
35 multiple feeding guilds. Some of these species are widespread pests while others are conservation
36 targets. They exhibit a remarkable diversity of defensive strategies and trophic ecologies, suggesting
37 varied adaptations for coping with cycad-specific phytotoxins. However, the biology of cycadivorous
38 Lepidoptera has never been reviewed, and the majority of relevant studies have concentrated on just
39 a few focal species without examining broader ecological or evolutionary patterns. The aims of this
40 review are therefore to 1) present an authoritative list of cycadivorous Lepidoptera and distinguish
41 verified from unverified records, 2) discuss key ecological and evolutionary implications of cycad
42 feeding in the context of broader plant-lepidoptera interactions, and 3) highlight important data gaps
43 and areas for future study.

44 Lepidopteran Cycad Herbivores

45 Cycadivory occurs in seven Lepidopteran families (Table 1), including the butterfly families
46 Nymphalidae and Lycaenidae. Among nymphalid butterflies, larvae of two species in the Australasian
47 genus *Taenaris*—*T. onolaus* and *T. butleri*—have been reported to feed on *Cycas* (species unknown) in
48 Papua New Guinea [29, 30]. In addition to larval cycad feeding, some adult *Taenaris* butterflies imbibe
49 cycad juices: *T. onolaus* and *T. catops* have been observed visiting fermenting cycad seeds, feeding on

50 exudates from wounded cycad leaves, and even probing the fresh frass of cycadivorous beetle larvae
 51 with their probosces [29]. This behavior is particularly remarkable in *T. catops*, the larvae of which feed
 52 on palms (Arecaceae) and are not known to be cycadivorous.

53 Three genera of lycaenid butterflies—*Luthrodes*, *Eumaeus*, and *Theclinesstes*—include species that
 54 are obligate cycad herbivores. The *Luthrodes* - *Chilades* clade is comprised of two sister genera that
 55 have historically been lumped together (typically under name *Chilades*). Here we follow Talavera *et al.*
 56 (2013) and treat them as separate genera [31]. Thus, we consider the cycadivorous lycaenid species
 57 that are typically referred to in the literature as *Chilades* to be properly placed in *Luthrodes*: *L. pandava*,
 58 *L. peripatria*, and *L. cleotas*. *Luthrodes pandava* is widespread across southern and southeast Asia and the
 59 larvae are often serious pests of *Cycas* [32]. *Luthrodes cleotas* also occurs in southeast Asia and feeds
 60 on *Cycas* [30], but less is known about its life history. The third species, *L. peripatria*, is endemic to
 61 Taiwan and its taxonomic status is unclear: some authors treat it as a full species ([31, 33]) while others
 62 consider it a subspecies of *L. pandava* ([34, 35]). The larvae of *L. peripatria* historically fed only on *Cycas*
 63 *taitungensis*, also endemic to Taiwan, though it now accepts the ornamental species *Cycas revoluta* [35]
 64 which has been introduced to Taiwan in large numbers since the 1990s [34].

65 The neotropical lycaenid genus *Eumaeus* is comprised of six species distributed from Peru to the
 66 Caribbean [36], with *E. atala* extending into southeastern Florida and some (perhaps dubious) records
 67 of rare strays of *E. toxea* into southern Texas [37]. All six *Eumaeus* species are obligate cycad herbivores,
 68 utilizing cycads in the neotropical genera *Zamia*, *Dioon*, and *Ceratozamia* [38–43]. Larvae of several
 69 *Eumaeus* species have been observed feeding on plants' fresh male and female reproductive cones in
 70 addition to stem and leaf tissue [43–48], and we know of a single report of *E. childrenae* adults feeding
 71 on cycad exudates [49]. Finally, *Theclinesstes* is a mostly Australian genus of six species, of which one
 72 species, *T. onycha*, feeds on cycads in the genera *Cycas* and *Macrozamia* in eastern Australia [20].

73 Among moths, 23 species from 8 genera have been recorded on cycads but this is likely an
 74 underestimation, as many cycad-feeding moths remain poorly collected and understudied. An
 75 entire tribe of Geometrid moths, the Diptychini, consists of 17 cycadivorous species in 3 genera [50].
 76 Colloquially called "the cycad moths," these are the best studied of the cycadivorous moths and are
 77 the only cycadivorous Lepidoptera known from Africa. The hostplants of all Diptychini larvae are
 78 *Encephalartos* and *Stangeria* cycads for the first 3 instars, but larvae in later instars often switch to
 79 angiospermous host plants [51–53]. Hostplant species for Diptychini moths are therefore separated
 80 into primary (cycad) and secondary (non-cycad) hosts in Table 1.

81 In addition to these obligate cycad herbivores, a number of facultative cycadivores exist.
 82 *Seirarctia echo* (Erebidae) occurs in the southeastern United States where the larvae are highly
 83 polyphagous, feeding on leaves of the cycad *Zamia integrifolia* as well as plants in the families Arecaceae,
 84 Euphorbiaceae, Fabaceae, Fagaceae, and Ebenaceae. In captivity, they have even been reared on lettuce
 85 (Asteraceae) [54]. One undetermined leaf-mining *Erechthias* moth (Tineidae) has been found feeding
 86 and pupating in the leaves of *Cycas micronesica* in Guam [55]. Larvae of *Dasyses rugosella* (Tineidae) have
 87 been observed feeding on dead *Cycas* stems in India, Sri Lanka, Thailand, Indonesia, and Guam [55, 56].
 88 Colloquially called "yam moths," *D. rugosella* are best known as pests of stored yams in West Africa
 89 [57, 58], and are broad generalists on decaying vegetable matter [59]. Larvae of *Anatrachyntis badia*
 90 (Cosmopterigidae), another highly polyphagous and cosmopolitan moth species, have been found in
 91 pollen cones of *Zamia integrifolia* in Florida, USA [60] and feeding on leaves of *Cycas revoluta* and *C.*
 92 *circinalis* in Italy [61]. An undetermined *Anatrachyntis* species pollinates *Cycas micronesica* in Guam and
 93 feeds on pollen cones as larvae [62, 63]. Finally, larvae of an undetermined microlepidopteran in the
 94 family Blastobasidae have been found feeding in copious numbers on pollen cones of *Zamia pumila*
 95 in the Caribbean [64].

96 Many records exist for lepidopteran species feeding on cycads which are likely to be erroneous or
 97 require further confirmation. We discuss these in the Supporting Information. The species listed in
 98 Table 1 have been identified by experts, confirmed by multiple sources, supported with photographic
 99 evidence, and in many cases their larvae have been reared in captivity on cycads. However, while

we feel that this paper serves as an authoritative list of cycadivory among Lepidoptera, it is likely not an exhaustive account of all cycadivorous species considering that new records of cycad-insect associations are still being reported (e.g., [60]), particularly among cone-feeding microlepidoptera.

Defensive Ecology

Cycad secondary chemistry

Cycads produce several toxic compounds in their leaves and other tissues, including steryl glycosides, β -Methylamino-L-alanine (BMAA), and methylazoxymethanol acetate (MAM) [65–69]. These compounds are toxic to most animals [70] and are therefore presumed to function as anti-herbivore defenses, though MAM is the only compound for which experimental evidence exists for insect deterrence [71–73]. MAM occurs in cycad tissues in a non-toxic glycosylated form and is known by different names (e.g., cycasin, macrozamin) depending on its sugar moiety. Defensive glycosides are widespread in several angiospermous plant families and include cyanogenic glycosides, cardiac glycosides, iridoid glycosides, salicinoids, glucosinolates, and others [74]. Many of these compounds have convergently evolved in distantly related plant families, whereas cycads are the only plants known to produce MAM. As a two-component chemical defense, MAM's toxicity is activated by β -glucosidase enzymes that cleave the protective sugar moiety from the toxic aglycone [65, 75]. MAM then spontaneously degrades into formaldehyde and methyl diazonium, with mutagenic, carcinogenic, and neurotoxic effects [65, 66]. Numerous non-cycadivorous Lepidoptera ingest and even sequester plant-derived two-component defensive chemicals for their own protection from natural enemies: for example milkweed-feeding butterflies and moths (subfamilies Daninae and Arctiinae, respectively) sequester cardenolides; some species in the Nymphalidae, Geometridae, Sphingidae and Arctiinae sequester iridoid glycosides; cyanogenic glycosides are sequestered by species in the Heliconiinae, Acraeinae, and Zygaenidae; and some Pieridae larvae sequester glucosinolates [76, 77]. Early work by Teas showed that larvae of the cycadivorous moth, *Seirarctia echo* (subfamily Arctiinae), are able to chemically modify MAM into its glycosylated form and accumulate non-toxic MAM-glycosides in their tissues after feeding on cycad leaves [78, 79], but the molecular mechanism(s) by which they do so is unknown. It is possible that other cycadivorous Lepidoptera are capable of similar chemical modifications though this has never been tested.

β -Methylamino-L-alanine is a non-protein amino acid found in cycad tissues, but is also produced by cyanobacteria in aquatic, marine, and terrestrial environments [80, 81]. All cycads engage in endosymbioses with cyanobacteria, which are housed in specialized coralloid roots and are thought to provision plants with fixed nitrogen (and potentially other specialized metabolites) in exchange for carbon and physical protection [82, 83]. Given that BMAA is produced by free-living cyanobacteria in other habitats, its biosynthetic source in cycads has been debated [84, 85]. As a potent excitotoxin, BMAA interferes with glutamate receptor function and can misincorporate into proteins, and the ingestion of foods containing BMAA has been implicated as a possible cause of amyotrophic lateral sclerosis, Alzheimer's disease, Parkinson's disease, and other neurodegenerative diseases in humans [67, 84, 86, 87]. Toxic effects of BMAA have been demonstrated in mammals [70, 88, 89], insects [90–92] and crustaceans [81], fish [93, 94], microbes [93], and plants [95]. Hundreds of non-protein amino acids have been identified in other plant families, especially legumes and grasses, and while the functions of these compounds are highly variable and often uncharacterized, many are believed to serve as anti-herbivore defenses [96–98]. The possible function(s) of BMAA in cycads—defensive and otherwise—have never been experimentally demonstrated, though based on its demonstrated toxicity to diverse organisms most researchers presume that BMAA serves as a defense against herbivores. Mechanisms of resistance to BMAA have not been investigated for any lepidopteran, though there is evidence that cycadivorous weevils are able to avoid BMAA by consuming only pollen cone parenchyma tissue where BMAA is thought to be sequestered in specialized cells that the weevils excrete in their frass [99, 100]. In addition to MAM and BMAA, cycads produce steryl glucosides

148 and numerous other chemicals whose roles in plant-herbivore interactions have yet to be sufficiently
149 characterized.

150 *Insect defensive ecology*

151 Cycadivorous Lepidoptera appear to tolerate all cycad toxins and several species are brightly
152 colored, diurnal, and gregarious—traits commonly associated with chemically defended Lepidoptera
153 (Figure 1) [101]. Indeed, previous studies have shown that some cycadivorous species sequester
154 MAM-glycosides into their larval and adult tissues. Rothschild, Nash, & Bell (1986) found that
155 *Eumaeus atala* larvae, pupae, and adults contained MAM-glycosides in surprisingly high amounts
156 relative to their hostplants [75], and Castillo-Guevara & Rico-Gray (2003) detected MAM-glycosides
157 in the eggs, larvae, pupae and adults of *Eumaeus* sp. (probably *toxea*) in Mexico [102]. Nash *et al.*
158 (1992) quantified MAM-glycosides in dried museum specimens of adult butterflies, including some
159 specimens that were over 70 years old [103]. The authors detected MAM-glycosides in *Eumaeus minyas*
160 (male and female), *Luthrodes cleotas* (male and female), *Taenaris butleri* (male and female), *Taenaris catops*
161 (male), and *Taenaris onolaus* (female) but did not detect MAM-glycosides in *Theclinessthes onycha* (either
162 gender), female *Taenaris catops*, or male *Taenaris onolaus*. They concluded that MAM-glycosides were
163 not detectable from the latter two because of the advanced age of the museum specimens, but that
164 *Theclinessthes onycha* probably do not sequester MAM-glycosides.

165 Since several of the species that sequester MAM-glycosides are brightly colored, their coloration
166 may be considered aposematic. Aposematism and chemical defense are exceedingly rare traits among
167 lycaenid larvae [75, 104, 105], which typically rely on crypsis and ant association for protection against
168 natural enemies [21]. *Eumaeus* provide a striking exception in that they are gregarious and warningly
169 colored in all lifestages, are known to sequester cycad toxins, and do not form larval associations
170 with ants [106]; whereas larvae of other cycadivorous lycaenids commonly associate with ants and
171 are cryptically colored [107–109]. Larvae of *Luthrodes cleotas* are cryptically colored but adults have
172 much larger orange spots on their hindwings than do their congeners, and it is possible that they are
173 aposematic, particularly given that adults have been shown to sequester MAM-glycosides [103].

174 Larvae and adults of Dyptichini moths are brightly colored with gregarious larvae and diurnal
175 adults, but it is unclear whether they sequester plant toxins at any life stage (Donaldson & Basenberg
176 (1995) suggest that *Z. lepida* sequester MAM-glycosides, but do not provide experimental evidence
177 [52]). *Seirarctia echo* larvae are warningly colored and covered with protective hairs. This species
178 sequesters MAM-glycosides when feeding on cycads [78, 79], but it remains unknown how feeding
179 on non-cycad hostplants affects their palatability and predation risk. Finally, *Anatrachyntis* moths
180 and the other microlepidoptera are not aposematic in any lifestage and many species spend their
181 entire development concealed inside plants' pollen cones, where they may avoid some cycad toxins
182 [100, 110]. It is completely unknown whether leaf-mining *Erechthias* and detritivorous *Dasyses* larvae
183 encounter cycads' defensive compounds while feeding.

184 Unfortunately, records of predators and parasitoids are lacking for nearly all cycadivorous species.
185 Natural enemies of Lepidoptera generally include birds, small reptiles, spiders, mantids, reduviid bugs,
186 ants, and parasitic wasps and flies, though direct observations of attacks on larvae and adult butterflies
187 are exceedingly rare [111]. The best-studied cycadivorous species with regard to defensive ecology is
188 *Eumaeus atala* in southeastern Florida. Both native and non-native ants have been observed consuming
189 *E. atala* eggs and pupae [112], but are thought to avoid adult butterflies [71]. Some assassin and ambush
190 bugs (Reduviidae) will attack *E. atala* larvae [113] although published records are scarce. Unconfirmed
191 reports exist of native and non-native reptiles attacking *E. atala* larvae and adults. Starlings, peacocks,
192 and other non-native birds have been reported to attack caterpillars, though it's possible that only
193 naïve birds will attempt to eat *E. atala*, as adult butterflies were shown to be distasteful to grey jays
194 [114]. There are no reports of parasitoids using *E. atala* as hosts, a conspicuous absence given that
195 parasitoids are typically significant natural enemies of lepidopteran larvae.

196 Ruiz-García *et al.* (2015) monitored survival and development of *Eumaeus toxea* larvae in Oaxaca,
 197 Mexico and observed *Dasydactylus* beetles preying on molting *E. toxea* larvae but did not report finding
 198 any parasitoids [47]. In contrast, Manners (2015) reports that "high levels of parasitism" sometimes
 199 occur in *Theclinesthes onycha* larvae in Australia, and provides photographs of larvae parasitized by
 200 braconid wasps [115]. The only published records of parasitization among cycadivorous moths come
 201 from *Zerenopsis lepida*: Staude *et al.* (2014) reared a single parasitoid fly (Tachinidae) from a late instar
 202 larva in South Africa [53], and Sommerer (2014) reared 15 *Z. lepida* larvae and found more than 50
 203 percent had been parasitized by *Charops* sp. (Ichneumonidae) or *Drino* sp. (Tachinidae) [116]. Aside
 204 from these scattered records we know relatively little about the natural enemies of cycadivorous
 205 Lepidoptera in the wild, including the importance of entomopathogenic microbes. Moreover, the
 206 effectiveness of aposematism and other defensive strategies against vertebrate, invertebrate, and
 207 microbial enemies remains an outstanding issue, even among well-studied Lepidoptera.

208 Evolutionary Origins of Cycadivory

209 To evaluate evolutionary origins of cycadivory and relationships among cycadivorous
 210 Lepidoptera, cycadivory was mapped on to a phylogenetic tree constructed by combining a
 211 Lepidoptera phylogeny [117] including butterflies and moths with a heavily sampled butterfly
 212 phylogeny [118] (Figure 2). Both phylogenies were downloaded as .nex files from published sources
 213 and brought into R (version 3.5.1) [119] where the butterfly clade from Espeland *et al.* (2018) [118] was
 214 substituted in place of the less sampled clade from Regier *et al.* (2013) [117] using the R packages ape
 215 [120], GEIGER [121], and ggtree [122, 123]. In cases where cycadivorous species were not represented
 216 as tips on the tree, the represented tip of the closest relative was identified using published phylogenies
 217 of families or genera [31, 50, 124–126].

218 A visual inspection of the Lepidoptera phylogeny suggests that cycadivory has evolved
 219 independently in multiple lepidopteran lineages, with several origins likely within single families
 220 and potentially even single genera. For example, a poorly resolved phylogenetic hypothesis based on
 221 morphological data for *Taenaris* does not place the two cycadivorous species within a monophyletic
 222 clade or closely related to each other [30], suggesting multiple origins of cycadivory in the genus.
 223 Similarly, an unpublished molecular phylogeny that includes some species of *Luthrodes* does not place
 224 the two included cycadivorous species as sister clades [127]. Conversely, cycadivory appears to be
 225 an ancestral trait in *Eumaeus* butterflies (6 species) and Diptychini moths (17 species). Given that
 226 both of these clades are warningly colored and obligately cycadivorous, it seems likely that cycad
 227 feeding or defensive traits (or both) have led to limited radiations in these groups. Dated phylogenetic
 228 hypotheses for all genera would be required to understand the general evolutionary significance of
 229 cycadivory and why some lineages have diversified while others are represented by just one or two
 230 species nested within otherwise non-cycadivorous clades.

231 Given the evolutionary history of cycads and phylogenetic placement of cycadivorous
 232 Lepidoptera, it is likely that transitions to cycadivory among extant cycadivorous Lepidoptera occurred
 233 within the last 15 to 20 million years. Indeed, at least in lyceanid butterflies the evolutionary origins
 234 of cycadivory appear to be somewhat recent. Talavera *et al.* 2013 dates the split between *Luthrodes*
 235 and its sister genus *Chilades* at ~6 MY [31], but the cycadivorous species of *Luthrodes* included in the
 236 analysis are derived, placing the origin(s) of cycadivory in this lineage as even younger. Similarly,
 237 an unpublished molecular clock analysis in *Theclinesthes* estimates the origin of the genus at 2-3 MY
 238 [128]. Finally, Espeland *et al.* (2018) places the split between *Eumaeus* and *Calycopis* at ~18 MY [118],
 239 making the origin of *Eumaeus* even more recent as this analysis did not include *Eumaeus*'s sister genus
 240 *Theorema*.

241 Improved phylogenetic estimates for cycadivorous Lepidoptera would be useful for reconstructing
 242 and comparing historical diet evolution among cycadivorous lineages, though research in this
 243 area is hindered not only by the unavailability of genus-level phylogenetic reconstructions, but
 244 also by incomplete or erroneous hostplant records for many species (see Table S1 in Supporting

Information). Some have speculated that monocot-feeding may be an evolutionary precursor to cycadivory because non-cycadivorous *Taenaris* feed on monocots [129], though there is little evidence from other groups to support this as a broad pattern. Among lycaenids, close relatives of cycadivorous species feed on dicots in the families Fabaceae, Amaranthaceae, Proteaceae, Sapindaceae, Myrtaceae, and Euphorbiaceae [20, 130]. Cycadivorous moths and their close relatives exhibit a broad range of hostplant preferences that includes both monocots and dicots. Improved knowledge of the evolutionary histories of cycadivorous lineages would provide a framework for testing hypotheses about evolutionary precursors to cycadivory and host breadth among extant species.

Hostplant Use

Based on the records reported here, cycadivorous Lepidoptera utilize 7 of the 10 recognized cycad genera [26] (Figure 3). Absent among accepted hostplant genera are *Lepidozamia*, *Bowenia* and *Microcycas*. These are all small genera (*Lepidozamia*: 2 species; *Bowenia*: 2 species; *Microcycas*: 1 species).

All cycadivorous butterflies appear to be obligate cycad specialists while cycadivorous moths exhibit a broader range of dietary preferences. *Seirarctia echo* is the only confirmed facultative cycad folivore, accepting leaves from a wide variety of hostplants from several plant families. The ecological causes and consequences of feeding on cycad versus non-cycad plants are completely unexplored in this species. Diptychini moths are facultatively polyphagous in their 4th–6th instars but all species are obligate cycad specialists for the first 3 instars. Donaldson & Basenberg (1995) found no significant differences in survival rate, developmental duration or pupal mass between 4th instar *Z. lepida* larvae reared on angiosperm versus cycad hosts [52]. Staude (2014) has suggested that some Diptychini moths may not require cycads even in their early stages, as he collected a single final-instar *Z. tenuis* larva feeding on the leaves of a baobab tree (*Adansonia digitata*, Malvaceae) on Misali Island, Tanzania, where no cycads were found [53]. The remaining cycadivorous moth species are either highly polyphagous (e.g., *Dasytes rugosella*) or their host breadth is unknown (e.g., *Erechthias* sp.).

Whereas not all cycadivorous Lepidoptera are specialists of cycads, their larvae are specialized on particular plant tissues and can therefore be categorized into discrete feeding guilds. These guilds include leaf chewers, leaf miners, ovulate cone feeders, pollen cone feeders, and detritivores, and the larvae in each of these guilds likely experience qualitative and quantitative differences in exposure to cycad toxins. For example, pollen cone feeders may experience reduced exposure to toxins since at least one cycad toxin, BMAA, appears to be sequestered in specialized cells in the pollen cones that can pass through the guts of other insects intact [100, 110]. Detritivorous species feed on decaying cycad pollen cones and stems that may also harbour lower concentrations of toxins. In contrast, *Eumaeus* butterfly larvae feed on both ovulate and pollen cones as well as leaves [45, 46], and some evidence suggests that *Z. lepida* moths also feed on ovulate cones in addition to leaves [131]. The seeds of some cycad species are known to contain high concentrations of MAM and BMAA relative to other plant tissues [132–134] and ovulate cones do not sequester BMAA into specialized cells [100, 110]. It is therefore unsurprising that only obligate cycad specialists can utilize ovulate cones, particularly those species which are known to sequester MAM.

Among cycad specialists, it appears that larvae can accept diverse cycad species and hostplant breadth is expanding for several species, particularly as exotic cycads are planted as ornamentals in gardens worldwide. The Caribbean species *Eumaeus atala*, for example, historically fed only on Caribbean cycads in the genus *Zamia*, but have been observed laying eggs and feeding on cultivated Central American cycad species that are outside of the native range, as well as some species of African, Australian, and Asian cycads [39, 43]. The ability to feed on non-native cycads has been observed in other *Eumaeus* species as well [48], and increased hostplant breadth has been reported for *Luthrodes pandava*, a widespread pest that feeds on numerous native and exotic cycads across Asia and the Middle East [34, 135–137].

Contemporary host use may challenge the species status of *Luthrodes peripatria*, which some authors consider to be a subspecies of *Luthrodes pandava*. The natural range of *L. pandava* is widespread

294 across southern Asia (excluding Taiwan), whereas *L. peripatria* is endemic to Taiwan and has historically
 295 fed on a single cycad species restricted to southeastern Taiwan, *Cycas taitungensis* [138]. In the past
 296 30 years, *L. pandava* has been introduced to Taiwan along with several exotic *Cycas* species. As both
 297 *Luthrodes* species accept native and non-native *Cycas* species as hostplants, expanded hostplant use and
 298 range overlap could provide opportunities for interbreeding. Further assessment of the population
 299 structure, introgression, and species status of *L. pandava* and *L. peripatria* would be fruitful (but see
 300 [34]).

301 Hostplant specialization may promote divergence in the Australian species *Theclinesstes onycha*,
 302 for which two subspecies are recognized, *T. onycha onycha* and *T. onycha capricornia*. *T. o. onycha* feeds
 303 only on *Macrozamia* cycads distributed from southern Queensland to New South Wales whereas *T.*
 304 *o. capricornia* feeds only on *Cycas* species in Northeast and central Queensland. They overlap in
 305 their distributions in a narrow region in central Queensland, though microhabitat preferences may
 306 maintain allopatry even within this contact zone. Patterns of hostplant use and mate choice are not well
 307 described within the contact zone, though Eastwood (2006) found considerable genetic differentiation
 308 in the mitochondrial genes of each subspecies, suggesting that there is little to no gene flow between
 309 them [128].

310 Careful analysis of hostplant use, species relationships, and reproductive barriers would also
 311 be useful for the two pairs of sympatric species of *Eumaeus* butterflies in Central and South America.
 312 *Eumaeus childrenae* and *E. toxea* co-occur in some parts of their ranges in Mexico, where they are easily
 313 distinguished based on wing pattern. These species are likely quite diverged and they utilize different
 314 cycad genera as hostplants throughout much of their range, though detailed studies of host use in
 315 areas of sympatry and allopatry have not been carried out. *Eumaeus toxana* and *E. minyas* both occur in
 316 South America and according to published records their ranges overlap in Peru. However, it is difficult
 317 to glean even basic natural history information for these two species due to widespread mistakes in
 318 species identifications in the published literature. *Eumaeus minyas* is commonly confused with several
 319 other *Eumaeus* species, especially *E. toxana* and the isthmus species *E. godartii*, but also *E. toxea* and
 320 even *E. atala*. Credible accounts of the distributions and range limits for *E. minyas* and *E. toxana* are
 321 needed, with *E. toxana* being particularly under-collected and poorly studied.

322 Among Caribbean species, the ranges of *Eumaeus atala* and *Seirarctia echo* overlap in southern
 323 Florida but there are very few records of both species occurring in the same place, suggesting that
 324 there is some displacement at a relatively fine spatial scale. Since *S. echo* is broadly polyphagous,
 325 hostplant competition is unlikely to be a sufficient explanation. Furthermore, the range of *E. atala* does
 326 not occupy the entire range of its hostplants in Florida, and a better understanding of the factors that
 327 determine the range boundaries of these species would be very valuable for the management of local
 328 butterfly and cycad populations.

329 Discussion

330 Cycadivorous Lepidoptera comprise a 'component community' of distinct lineages with varying
 331 degrees of specialization and diverse feeding ecologies, and therefore present numerous opportunities
 332 for comparative studies of eco-evolutionary dynamics (e.g., [139]). Additionally, because of their novel
 333 chemical and ecological features, cycads and their herbivores provide a valuable complement to the
 334 model systems that dominate plant-insect research. Based on this first review of the phylogenetic
 335 and natural histories of these species, we speculate here on some of the salient questions regarding
 336 cycad-Lepidoptera interactions.

337
 338 *Is cycad-feeding adaptive?* Evolutionary transitions to feeding on plants that contain defensive
 339 secondary compounds are claimed to promote diversification of Lepidoptera through escape and
 340 radiation (e.g., [17]). If cycadivory has similarly promoted diversification in lepidopteran lineages,
 341 then it might be considered an adaptive trait. Based on the phylogenetic pattern shown in Figure
 342 2, *Eumaeus* butterflies and Diptychini moths exhibit modest radiations following their transition to

343 cycad-feeding, whereas other cycadivores remain as only one or two species at the tips of otherwise
 344 angiosperm-feeding clades. Why have some cycadivorous lineages diversified while others have not?

345 That the largest clades of cycadivorous Lepidoptera are also aposematic suggests that defensive
 346 ecology may play a role in diversification: perhaps it is not cycadivory *per se* that leads to diversification
 347 in some lineages, but rather the subsequent evolution of aposematism. This explanation is consistent
 348 with the cryptic coloration of cycadivorous species that have not radiated, though a few exceptions
 349 must be considered. *Luthrodes cleotas* and *Seirarctia echo* are both known to sequester cycad toxins and
 350 could be considered warningly colored; why have these species not diversified? Cycadivorous *Taenaris*
 351 species are also warningly colored but do not appear to have radiated (though even non-cycadivorous
 352 *Taenaris* are considered aposematic [20] so this situation may be more complicated).

353 It may be that evolutionary trade-offs or constraints have limited diversification in these groups,
 354 that other cycadivorous relatives once existed but have gone extinct, or that cycadivory has evolved
 355 too recently for diversification to have yet taken place. Indeed, cycadivorous species of *Luthrodes* and
 356 *Theclinesthes* appear to be very young, and it would be interesting to compare their ages to those of
 357 *Eumaeus* butterflies and *Diptychini*. Among generalists, cycadivory is not expected to significantly
 358 influence speciation rates (at least for detritivorous moths), though *Seirarctia echo* and *Erechthias* sp.
 359 may be exceptions given that they possess specific adaptations for feeding on cycads' fresh leaf tissue.

360
 361 *Is there evidence of coevolution between cycads and their lepidopteran herbivores?* All
 362 cycadivorous Lepidoptera must possess adaptations to circumvent or tolerate cycad-specific defenses,
 363 and the selective value of cycad defensive traits against herbivores seems clear. But what of the
 364 selective influence of cycadivorous Lepidoptera for their host cycads? While there is little debate
 365 about the importance of plant defensive traits for herbivore fitness [140, 141], the importance of insect
 366 herbivores as selective agents is less clear as most plants seem able to tolerate intermediate levels of
 367 herbivory without a significant reduction in fitness [142]. Evidence of reciprocal adaptation between
 368 pairs of plants and herbivores has been relatively scarce [143], and the step-wise selection scenario
 369 initially envisaged by Ehrlich & Raven appears to be extremely asymmetrical: shifts to chemically
 370 novel hosts lead to bursts in diversification in many herbivore groups, but escape from herbivores
 371 through chemical novelty seems to have had little impact on diversification rates in most plant groups
 372 [18, 144] (but see [145, 146]).

373 Still, damage inflicted by folivorous Lepidoptera can be so extreme that just a few generations can
 374 decimate a large cycad. Selective pressures exerted by some specialist herbivores may therefore be
 375 especially severe for cycads relative to other plant groups, raising the possibility that some lepidopteran
 376 herbivores could select for escalated chemical defenses and perhaps influence the diversification of
 377 their cycad hosts. Previous work has identified diverse secondary compounds in cycads [147, 148] that
 378 appear to be evolving [149], but phylogenetically explicit comparisons of cycad defensive chemistries
 379 (toxins, antinutritive compounds, and volatile organic compounds) would be required to look for
 380 evidence of phytochemical escalation.

381 The phylogenetic distribution of cycadivory in Lepidoptera suggests repeated, independent
 382 colonizations of cycads from distantly related angiosperm hosts, and the potential for co-speciation
 383 with cycads is reasonably plausible only among *Eumaeus* butterflies and *Diptychini* moths. Research in
 384 this area should therefore focus on assessing coevolution between *Eumaeus* with the new world cycad
 385 genera *Zamia*, *Dioon*, and *Ceratozamia*, and between the African *Diptychini* moths with cycad genera
 386 *Encephalartos* and *Stangeria*.

387
 388 *How does cycadivory evolve?* Identifying evolutionary and ecological precursors to cycadivory
 389 could help explain the repeated transitions to cycads among Lepidoptera. For example, did the host
 390 plants of ancestral species somehow facilitate shifts to cycad feeding, either through phytochemical
 391 similarity or other features? From the data presented here, there is no evidence that cycadivory has
 392 evolved from a single, shared host lineage. The ancestors of cycadivorous taxa likely fed on diverse

393 angiosperms including both monocots and dicots, though improved phylogeographic and life history
394 information will be required to infer the most likely ancestral food plants of each cycadivorous lineage.
395 Hypotheses regarding what the ancestors of cycadivorous species ate prior to their transitions to cycads
396 may suggest as yet unknown chemical similarities between cycads and some angiosperm groups. Or,
397 if no chemical similarities are found, it suggests potentially novel adaptations for overcoming cycads'
398 defenses.

399 Lepidoptera are known to employ numerous adaptations for feeding on chemically defended
400 host plants. These include behavioral adaptations [150], physiological mechanisms [151], and perhaps
401 even associations with symbiotic gut bacteria [152, 153] (otherwise considered exceptional among
402 Lepidoptera [24, 154]). Host switching and feeding on select plant tissues can also minimize an insect's
403 exposure to plant defensive compounds. For example, Diptychini moths – which we consider to be
404 obligate cycad specialists – commonly switch to feeding on angiospermous plants in late instars and
405 thereby potentially reduce their exposure to cycad defenses.

406 It is presently unknown which specific adaptations might be required for cycadivory, or how
407 widely specific adaptations are shared across and within feeding guilds, *e.g.*, among specialized
408 folivores. *Sierarctia echo* are capable of modifying dietary MAM into its non-toxic form [79], but it is
409 unknown whether other herbivores actively detoxify MAM using a similar mechanism. Moreover,
410 no adaptations have been identified to date that would enable herbivores to cope with BMAA, steryl
411 glycosides, or other defensive compounds, let alone complex phytochemical mixtures. Additionally,
412 herbivores need to locate and discriminate between potential host plants, and while previous work has
413 described chemical cues used by the insect pollinators of cycads [155], no research has investigated
414 chemical communication between cycads and lepidopteran herbivores.

415 Finally, different lepidopteran lineages may experience different evolutionary constraints in their
416 ability to feed on cycads. Among butterflies, the Nymphalidae appear to be relatively constrained
417 in their ability to colonize new hostplant families [156], whereas the Lycaenidae exhibit enormous
418 trophic diversity that includes both phytophagous and aphytophagous diets [21]. Indeed, Ehrlich &
419 Raven were able to identify few phylogenetic patterns in lycaenids' host use and were puzzled by their
420 'bewildering array' of host plant affiliations [1]. The only published lycaenid genome demonstrates
421 significant expansion in detoxification and digestion enzymes [23], which, if shared broadly across
422 the family, might explain why lycaenid butterflies seem predisposed to trophic innovation, including
423 repeated colonization of cycads over the last 20 MY. Yet despite their proclivity for unusual diets,
424 feeding on chemically defended host plants and sequestering host plant defensive chemicals is rare
425 among lycaenids [105], making the repeated evolution of cycadivory among lycaenids especially
426 exciting.

427 Conclusions

428 Cycadivorous Lepidoptera are remarkably diverse in their defensive strategies, life histories,
429 and hostplant relationships, providing numerous opportunities for future research. Their diets
430 span the full range of host specialization and there is evidence of host expansion in some species.
431 Cycad-feeding Lepidoptera include cases of possible incipient speciation and examples of likely
432 introgression, widespread pests as well as locally threatened species, and clades that are relatively
433 understudied in phytochemical ecology research (*e.g.*, lycaenid butterflies, Diptychini moths) along with
434 a few familiar standbys (*e.g.*, arctiid moths, nymphalid butterflies). Moreover, cycads possess defensive
435 chemistries that are not found in the angiosperm study systems that comprise the bulk of research
436 on plant-insect interactions. Some of these defensive chemicals appear to be influenced by cycads'
437 complex microbial associations and provide opportunities to investigate the effects of plant-microbe
438 interactions on plant-herbivore interactions, as well as the ecological and non-ecological significance
439 of non-protein amino acids, a widespread but relatively unstudied class of plant metabolites. The
440 resulting diversity in lepidopteran defensive traits, which range from camouflage to aposematism,
441 suggests both convergent and divergent adaptations to these toxins.

442 Yet despite several decades of research on a handful of focal species, many cycadivorous
443 Lepidoptera remain understudied, undersampled, and undescribed. In general, research in this area
444 would benefit from further investigations into cycad's defensive chemistries and insects' adaptations to
445 cycad toxins, systematic surveys of herbivore diversity and host breadth, and studies of predator and
446 parasitoid pressures in natural habitats, along with genus- and tribe-level phylogenies of cycadivorous
447 groups and their sister taxa. We highlight several promising research questions in Box 1. Future studies
448 would do well to consider other insect groups too, as cycadivory has been reported among larvae and
449 adults of non-pollinating beetles (Coleoptera) [55]; bees (Hymenoptera) [157–159]; leaf-mining larvae
450 of an unidentified fly (Diptera) [157]; termites (Blattodea) [160]; and phloem-feeding scale insects and
451 mealybugs (Hemiptera) [55, 72]. By summarizing what is known about the phylogenetic placement
452 of cycadivorous Lepidoptera, along with their hostplant relationships and defensive ecology, we
453 introduce them as a compelling study system with great promise for investigating the causes and
454 consequences of ecological interactions.

Box 1. Suggested Research Questions

- How widespread is sequestration of cycad defensive compounds among cycadivorous Lepidoptera? Which cycad toxins are sequestered and in which species, life stages, and tissues? What adaptations are required for deactivating, transporting, and/or storing MAM-glycosides and potentially other cycad toxins?
- Do insect-associated gut bacteria contribute to tolerance of cycads' defensive chemicals?
- Who are the natural enemies of cycadivorous Lepidoptera and how effective are lepidopteran defensive traits (*e.g.*, aposematism) against vertebrate predators, invertebrate predators, parasitoids, and entomopathogenic microbes?
- Do sequestered phytotoxins provide additional functions beyond defense for specialized Lepidoptera, *e.g.*, sexual pheromones, nutrient storage, biochemical signaling, etc.?
- What is the multi-trophic significance of cycadivory, and how do cycads' phytochemicals affect community structure and nutrient flow within ecosystems?
- Why do some lepidopteran clades appear more likely to evolve cycadivory than others? What evolutionary precursors, constraints, and trade-offs might be relevant to the evolution of cycad-feeding among Lepidoptera?
- What role do plant-associated microbes play in the defensive traits of cycads? For example, is BMAA produced by endosymbiotic cyanobacteria, by cycads, by both?
- What function(s) does BMAA provide in cycad metabolism and/or defense against herbivores?
- Can specialized insects' adaptations to BMAA-rich diets inform interventions relevant for human medicine and public health?

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Table 1. Larval hostplant records for cycadivorous Lepidoptera. See text for explanation of primary and secondary host use among geometrid moths. Species synonyms are given in Table 2 in Supporting Information. *Introduced plant species.

Species	Cycad Hosts	Other Hosts	Sources
Nymphalidae			
<i>Taenaris</i> Hübner, [1819]			
<i>T. butleri</i> (Oberthür, 1880)	<i>Cycas</i> (species unknown)		[29, 30]
<i>T. onolaus</i> (Kirsch, 1877)	<i>Cycas</i> (species unknown)		[29, 30]
Lycaenidae			
<i>Eumaeus</i> Hübner, [1819]			
<i>E. atala</i> (Poey, 1832)	<i>Zamia integrifolia</i> , <i>Z. vasquezii</i> *, <i>Cycas revoluta</i> *, <i>Encephalartos villosus</i> *, <i>Macrozamia lucida</i> *, at least 30 other non-native species		[39, 41, 43]
<i>E. childrenae</i> (Gray, 1832)	<i>Dioon edule</i> , <i>D. merolae</i> , <i>Ceratozamia matudae</i> , <i>C. mexicana</i> , <i>C. norstogii</i> , <i>C. robusta</i> , <i>C. chimalapensis</i> , <i>Zamia fischeri</i> , <i>Z. soconuscencis</i> , <i>Cycas revoluta</i> *		[38, 40, 42, 48]
<i>E. godartii</i> (Boisduval, 1870)	<i>Zamia acuminata</i> , <i>Z. fairchildiana</i> , <i>Z. manicata</i> , <i>Z. stevensonii</i>		[46]
<i>E. minyas</i> (Hübner, [1809])	<i>Zamia encephalartoides</i> , <i>Z. skimmeri</i>		[45, 161]
<i>E. toxana</i> (Boisduval, 1870)	Unknown		
<i>E. toxea</i> (Godart, [1824])	<i>Zamia furfuracea</i> , <i>Z. paucijuga</i> , <i>Z. encephalartoides</i> , <i>Z. loddigesii</i>		[47, 72, 162]
<i>Luthrodes</i> Druce, 1895			
<i>L. cleaotas</i> (Guérin-Méneville, [1831])	<i>Cycas</i> (species unknown)		[30]
<i>L. pandava</i> (Horsfield, [1829])	>85 species of <i>Cycas</i>		[32, 163, 164]
<i>L. peripatria</i> (Hsu, 1980)	<i>Cycas taitungensis</i> , <i>Cycas revoluta</i> *		[34]
<i>Theclimethes</i> (Röber, 1891)			
<i>T. onycha onycha</i> (Hewitson, 1865)	<i>Cycas megacarpa</i> , <i>C. ophiolitica</i> , <i>C. media</i>		[107, 165]
<i>T. onycha capricornia</i> Sibatani & Grund, 1978	<i>Macrozamia spiralis</i> , <i>M. communis</i> , <i>M. pauli-guilielmi</i>		[165]
Geometridae			
<i>Zerenopsis</i> Felder, 1874			
<i>Z. costimaculata</i> (Prout, 1913)	Primary hosts: <i>Encephalartos hildebrandtii</i>	Secondary hosts: unknown in the wild, <i>Diospyros lycioides</i> in captivity	[53]
<i>Z. flavimaculata</i> Staudé & Sihvonen, 2014	Unknown	Unknown	[53]
<i>Z. geometrina</i> (C. & R. Felder, 1874)	Primary hosts: <i>Stangeria eriopus</i> , <i>Encephalartos villosus</i>	Secondary hosts: <i>Apodytes dimidiata</i> , <i>Mimusops obovata</i>	[53]
<i>Z. kedar</i> (Druce, 1896)	Unknown	Unknown	[53]
<i>Z. lepida</i> (Walker, 1854)	Primary hosts: <i>Stangeria eriopus</i> , <i>Encephalartos</i> (>20 species), <i>Cycas thouarsii</i> , <i>C. circinalis</i> *, <i>C. revoluta</i> *, <i>Dioon</i> sp.*	Secondary hosts: <i>Carissa bispinosa</i> , <i>C. macrocarpa</i> , <i>C. bispinosa</i> , <i>Diospyros lycioides</i> , <i>D. whyteana</i> , <i>Apodytes dimidiata</i> , <i>Maesa alnifolia</i> , <i>M. lanceolata</i> , <i>Sclerocarya birrea</i>	[52, 53, 166]
<i>Z. meraca</i> (Prout, 1928)	Unknown	Unknown	[53]
<i>Z. moi</i> Staudé & Sihvonen, 2014	Primary hosts: <i>Encephalartos ferox</i>	Secondary hosts: unknown in the wild, <i>Diospyros lycioides</i> in captivity	[53]
<i>Z. tenuis</i> (Butler, 1878)	<i>Encephalartos hildebrandtii</i>	<i>Adansonia digitata</i>	[53]
<i>Veniliodes</i> Warren, 1894			
<i>V. inflammata</i> Warren, 1894	Primary hosts: <i>Stangeria eriopus</i> , <i>Encephalartos villosus</i>	Secondary hosts: <i>Apodytes dimidiata</i> , <i>Diospyros lycioides</i>	[166, 166]
<i>V. pantheraria</i> (C. & R. Felder, 1874)	Primary hosts: <i>Stangeria eriopus</i> , <i>Encephalartos villosus</i>	Secondary hosts: <i>Apodytes dimidiata</i> , <i>Diospyros lycioides</i>	[51, 166]
<i>V. setinata</i> (C. & R. Felder, 1875)	<i>Stangeria eriopus</i>		[166]
<i>Callioratis</i> C. & R. Felder, 1874			
<i>C. abraxas</i> Staudé, 2001	Primary hosts: <i>Encephalartos lebomboensis</i> , <i>E. altensteini</i> , <i>E. villosus</i>	Secondary hosts: <i>Apodytes dimidiata</i> , <i>Diospyros whyteana</i> , <i>Carissa</i> sp.	[166]
<i>C. apicisecta</i> Prout, 1915	<i>Stangeria eriopus</i> & <i>Encephalartos tegulaneus</i> in the wild, <i>E. villosus</i> in captivity		[166]
<i>C. curlei</i> Staudé, 2001	<i>Stangeria eriopus</i> , <i>Encephalartos friderici-guilielmi</i>		[166]
<i>C. grandis</i> Prout, 1922	<i>Encephalartos gratus</i>		[167]

Continued on next page

Table 1 – continued from previous page

Species	Cycad Hosts	Other Hosts	Sources
<i>C. mayeri</i> Staude, 2001	<i>Encephalartos friderici-guilielmi</i>		[166]
<i>C. millari</i> Hampson, 1905	Primary hosts: <i>Stangeria eriopus</i> in the wild, <i>Encephalartos villosus</i> in captivity	Secondary hosts: <i>Diospyros lycioides</i> in the wild, <i>Tropaeolum majus</i> flowers in captivity	[166]
Erebidae			
<i>Seirarctia echo</i> (Smith, 1797)	<i>Zamia integrifolia</i>	<i>Sabal palmetto</i> , <i>Diospyros</i> spp.*, <i>Quercus</i> spp., <i>Croton</i> spp., <i>Lupinus</i> spp., many other woody plants, lettuce	[54, 168]
Cosmopterigidae			
<i>Anatrachyntis</i> Meyrick, 1915			
<i>A. badia</i> (Hodges, 1962)	<i>Zamia integrifolia</i> , <i>Cycas revoluta</i> , <i>C. circinalis</i>	Dozens of species, including both angiosperms and gymnosperms	[60, 61, 169]
<i>A. sp.</i>	<i>Cycas micronesica</i>	Unknown	[55, 62, 63]
Tineidae			
<i>Dasytes rugosella</i> (Stainton, 1859)	<i>Cycas micronesica</i>	Dozens of plant species, mushrooms	[55, 59]
<i>Erechthias</i> sp.	<i>Cycas micronesica</i>	Unknown	[55]
Blastobasidae			
Undetermined	<i>Zamia pumila</i>	Unknown	[64]



Figure 1. Examples of aposematism among cycadivorous Lepidoptera. Photo credits from top to bottom: Shayla Salzman, Hermann Staude, William Tang.

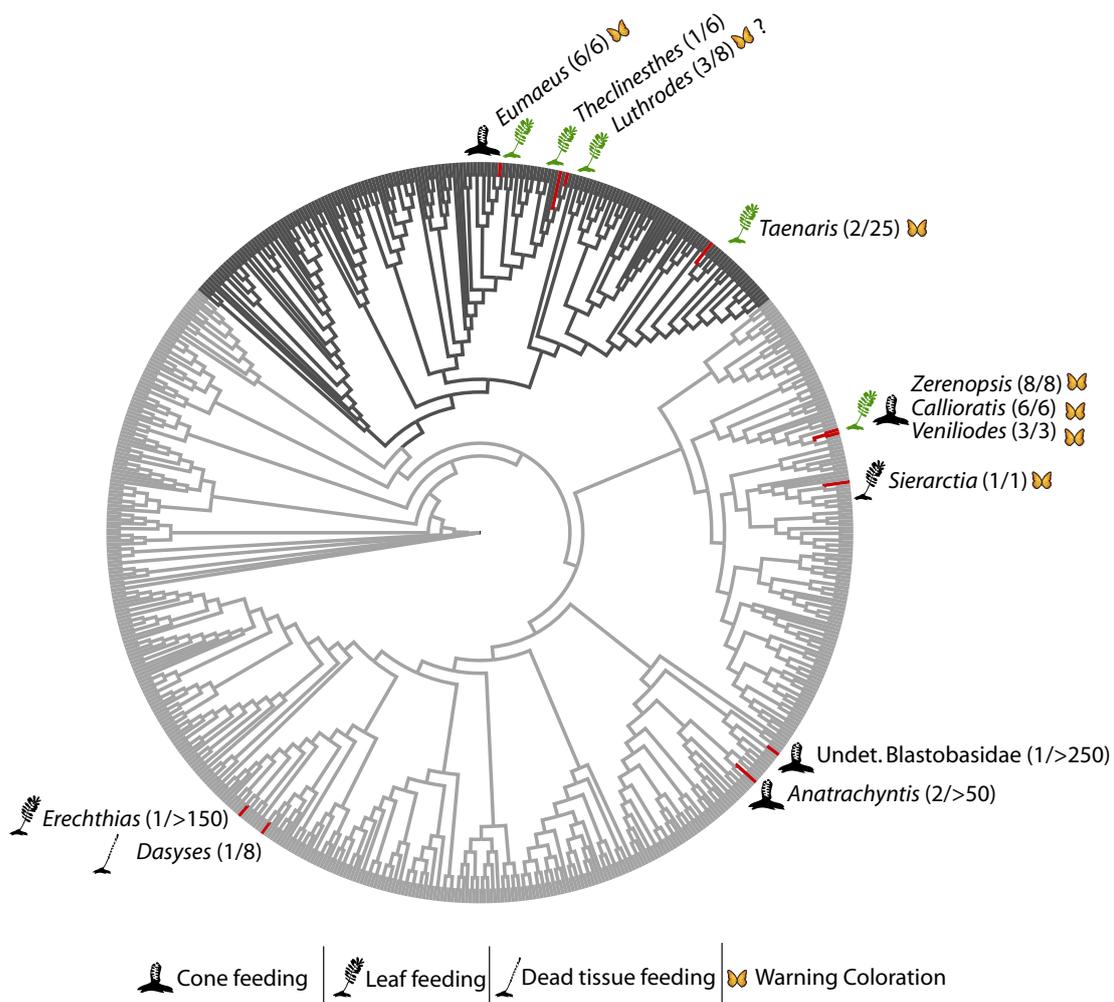


Figure 2. Phylogenetic placement of cycadivorous Lepidoptera. Genera containing cycadivorous species are shown by red tips, with the butterfly clade in black and moths in grey. Warning coloration is indicated symbolically, along with the feeding guild and whether a species is facultatively or obligately cycadivorous (black and green, respectively). The number of cycadivorous species and the total number of species in the genus are given in parentheses.

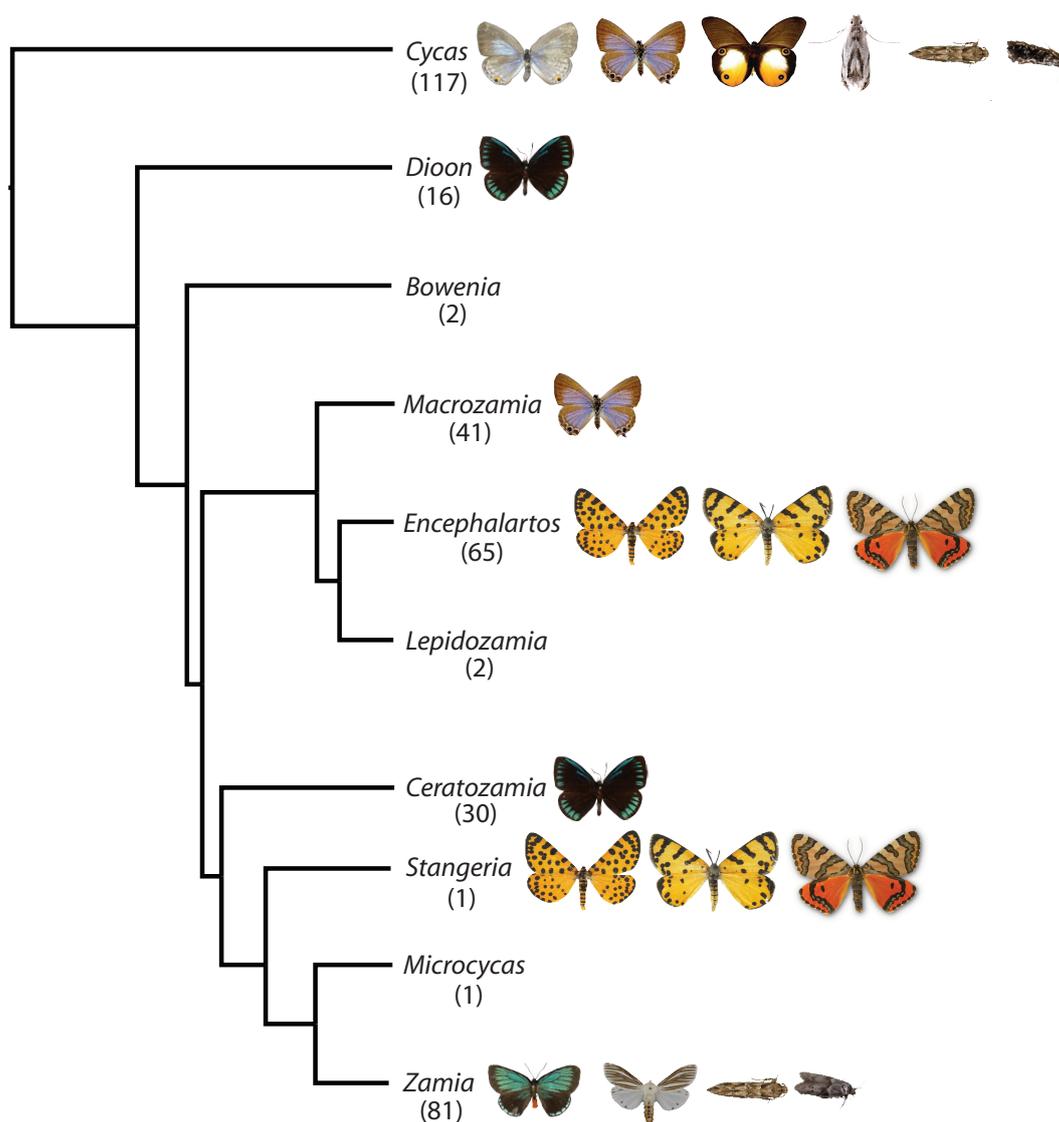


Figure 3. Cycad genera used as Lepidopteran host plants. Cycad phylogenetic tree from Salzman *et al.* [170]. Number of species in each plant genus is given in parentheses. Each lepidopteran genus is represented by one individual.

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